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The Ecology of Distraction Display

BY EDWARD A. ARMSTRONG

St. Mark's Vicarage, Cambridge

The category "Diversory display," involving all those activities which serve to deflect a potential predator from a bird's nest or young, includes two ritualised forms of distraction behaviour, injury-feigning or injury-simulation, in which a bird appears to be suffering from some disability, and types of eccentric or unusual gait or posturing, sometimes involving a greater or lesser resemblance to the appearance of another animal (Armstrong, 1949). Many predators are able to discriminate fine subtleties of movement and adornment (de Ruiter, 1952) and the remarkable realism of some injury-feigning displays illustrates the powerful selective effect of their attacks.

In a previous discussion (1949) I suggested that distraction display was the outcome of conflicting drives, on the one hand, the impulse to flee, and on the other, parental protective impulses—the latter often involving threat elements. Injury-feigning may thus be regarded as a ritualised compromise activity. Tinbergen (1952a) attributes distraction displays to "the simultaneous activation of the aggressive and escape drives" and Simmons (1952) thinks this is true of bird predator-reactions in general. As epigamic display may be performed by birds alarmed at the nest, e.g., Little Brown Cranes (*Grus canadensis*), (Brandt, 1943), it is probable that components of such displays have been incorporated into some distraction displays. However, the stage has been reached when the analysis of the distraction displays of individual species is needed in view of the indications that much display is the outcome of conflicting drives generating activities which, under selection, acquire signal functions. Thus, the distinction between sexual and threat elements and enticement and fleeing movements is often by no means clear cut. It should be

remembered that any activities of a parent bird which effectively deflect attention from the nest may function as diversory display and become modified in the process of ritualisation. Alarmed Black-winged Stilts (*Himantopus h. himantopus*) stand with their bodies vertical, waving their wings in what appears to be threat display (Beetham, 1914; Staton, 1945) and birds, disturbed at the nest may sing (Armstrong, 1947, 1950). Such behaviour, when effective in deflecting predators, could become stereotyped as diversory display. Marshall (1954) claims that song-mimicry is effective in this way but the evidence is inadequate to show that the mimicry involved gives efficacy to the performance.

Distraction displays are of very varied types so it will be convenient to concentrate attention here on injury-simulation and closely related forms of posturing because their elaborateness implies a considerable measure of evolutionary adaptation and they are among the most easily recognisable forms of distraction behaviour. Apart from a few suggestions by Allen (1936) and others, there has been no discussion of the relationship between such displays and the settings in which they are performed. Perhaps this may be attributed to the gaps in the information available but we have reached a stage when field observations and experimental work may be stimulated by an attempt, admittedly tentative, to consider the ways in which environmental conditions have affected the evolution and maintenance of these displays.

General Principles Underlying Injury-simulation Displays

The general principles governing injury-feigning displays may be illustrated by contrasting the nesting situations in which such displays are most, and least, accentuated:

Injury-simulation by breeding birds tends to be

most accentuated

- (a) in open, unprotected situations
- (b) when the nest is on, or close to relatively level ground.
- (c) when the nest is open and meagre.
- (d) in species nesting in isolation.
- (e) in species primarily subject to diurnal predation.
- (f) in high northern latitudes.

least accentuated

- in thick, varied vegetation.
- when the nest is in trees, high bushes, on a cliff ledge or closely surrounded by water.
- when the nest is (i) conspicuous, or (ii) of impenetrable material or protected by solid surroundings, as e.g. in a niche or cavity.
- in species nesting colonially.
- in species primarily subject to nocturnal predation.
- in the tropics.

Briefly, the birds for which distraction display is apt to be most advantageous are those with inconspicuous nests in vulnerable situations exposed to diurnal predators which can be evaded by flight.

The principles involved will be considered in order.

(a) *Injury-feigning has selective advantage when the nest or hiding-place of the young is on open and exposed terrain.*

In open environments brooding birds often have the advantage over predators of being able to perceive them before they are perceived, and collective mobbing sometimes enables birds over a wide area to be alerted (Kearton, 1915). They may crouch to gain additional concealment, slip unobtrusively from the nest, or fly away. When injury-simulation is performed the site chosen can be far enough from the nest not to disclose its position and sufficiently open for the parent to be able, not only to attract the predator's attention but to lead the animal away. Birds such as the Killdeer (*Charadrius vociferus*), Spotted Sandpiper (*Tringa macularia*), Stone Curlew (*Burhinus oedipnemos*) and Ruffed Grouse (*Bonasa umbellus*) may even run or fly towards the intruder in order to display (Deane, 1944; Mousley, 1937; Woodward, 1938; Thompson, 1896). Moreover, in bare surroundings there are plenty of places where the bird may perform conspicuously, whereas in thick vegetation, into which it can disappear unobtrusively, this may be difficult or impossible. In the American tropics birds which nest in dense vegetation do not injury-feign and species which usually perform do not do so in the absence of an open space for their act (A. F. Skutch, *in litt.*). A. H. Chisholm (*in litt.*) informs me that he saw a pair of Australian White-fronted Chats (*Ephthianura albifrons*) endeavour to perform injury-feigning in the air when no clear space was available.

The relevance of bare terrain in the evolution of injury-feigning is apparent when we note that this principle applies independently of latitude and the kind of substratum on which the eggs are laid—tundra, steppe, shingle, mud-flat or desert. In all latitudes birds of open terrain tend to injury-feign more than those nesting in thick vegetation in the same latitude. However, each of the principles here discussed is qualified by, and qualifies, other principles. Thus, although some desert birds, such as Sand Grouse (*Pterocles* and *Syrhaptes*) injury-feign (Meinertzhagen, *in litt.*; Ali, 1949) such be-

haviour is less general than in tundra species, due, probably, to the frequent choice of partially protected nesting sites and, more particularly, to non-avian desert predators being less diurnal than those of tundra. Snakes, and many other animals, become crepuscular or nocturnal in desert areas (Schmidt and Davis, 1941). The Arctic Fox (*Alopex lagopus*) hunts at all hours during the birds' breeding season. Further south the Fox (*Vulpes vulpes*) hunts partly by day but mainly by night. The Fennec (*Fennecus zerda*) of North Africa is almost completely nocturnal. Although injury-feigning is performed by many ground-nesting passerines with nidicolous young it is most highly developed in, and is presumably most advantageous to, nidifugous species breeding on open terrain. The significance of this lies in the inefficacy of threats, or even attacks, if the predator remains in the neighbourhood of the young and is thus liable to find one or more. Thus the young of birds as various as the Ptarmigan (*Lagopus lagopus*), nightjars and nighthawks (*Caprimulgidae*), and Short-eared Owl (*Asio flammeus*), (Armstrong & Phillips, 1925), tend to disperse as soon as they are able. Distraction display is commonly most accentuated about the time when the young leave the nest—which approximates also to the time of hatching in nidifugous birds. There are exceptions, among which the extremes are represented by Little Pratincoles (*Glareola lactea*) and Killdeer which may injury-feign before the eggs are laid (Seebohm, 1885; Deane, 1948), Wheatears (*Oenanthe oenanthe*) which have been known to perform after the eggs had been taken (Meinertzhagen, 1938), Dotterel (*Charadrius morinellus*) and Arctic Skuas (*Stercorarius parasiticus*) which may continue to display after the young are on the wing (Haviland, 1917; Perry, 1948) or have died (Williamson, 1951).

(b) *The adaptive value of injury-feigning tends to increase according to the degree to which the nest is accessible to non-avian predators.*

Distraction display is most characteristic of birds nesting on or near the ground. It is performed by the ground-nesting cranes (*Balearicidae*) but not by tree-nesting herons and egrets (*Ardeidae*), by nightjars and nighthawks but not by swifts (*Apodidae*). It is much more characteristic of the ground-nesting Reed Bunting (*Emberiza schoeniclus*) than of the Cirl Bunting (*E. cirlus*) which chooses higher sites. Instances of injury-feigning by birds nesting in bushes, or, less commonly, in trees, cited by

Allen (1936), Chisholm (1936, 1948), Grimes (1936), Jourdain (1936), Moreau (1937), Potter (1936), Roberts (1944), Van Someren (1944) and others, do not invalidate the principle. A number of species mentioned by these writers usually nest within a short distance of the ground or behave in a manner which is hardly entitled to be called injury-feigning, but some of the exceptions to the rule that distraction display is uncommon among tree-nesting birds are of special interest. In this connection the most remarkable group is the Parulidae or American Wood Warblers. Injury-feigning is general among them and has been recorded of at least fifteen species which nest in bushes or trees (Cottam, 1936; Grimes, 1936; Rutter, 1936; Bent, 1953). Some of these birds, such as the Magnolia, Eastern Myrtle and Pine Warblers (*Dendroica magnolia*, *D.c. coronata* and *D. pinus*) topple and flutter from considerable heights and then shuffle along the ground as if disabled.

The Parulidae are of North American origin and confined to the New World (Lönnerberg, 1927; Mayr, 1946). As no Old World group exhibits such accentuated injury-feigning from heights it is interesting to enquire whether any form of arboreal predation is more frequent in one region than the other. We find that although the U.S.A. is about one-twelfth less in area than Europe it possesses about six times as many species of snake. In Florida, for example, there are at least five arboreal species known to eat birds and their eggs (Schmidt & Davis, 1941) while in Europe there are very few arboreal snakes. Bigglestone (1913), Grinnell & Storer (1924) and Sturm (1945) have published details of attacks by snakes on tree-nesting American warblers. Such data do no more than suggest that snakes may be largely responsible for injury-feigning among the Parulidae but they encourage the belief that, at least in some groups, the evolutionary history of such behaviour may be traced.

The relative infrequency of injury-simulation among tree-nesting birds may be partly due to the difficulty of performing in a plausible way on a twig or branch. Outside the Parulidae and apart from one striking observation of a Willow Warbler (*Phylloscopus trochilus*), (Siddall, 1910) few convincing instances have been recorded. Arboreal predators cannot readily be lured along branches beyond the limit of safety and, returning down the tree, are likely to find nests which, in such situations,

are often more conspicuous viewed from above than from below.

The virtual absence of injury-simulation among birds nesting on cliff ledges is due to the inaccessibility of such nests to non-avian marauders.

The rarity of injury-feigning among species with nests closely surrounded by water may be ascribed to the comparative ease with which such birds and their chicks can conceal themselves from a marauder or otherwise evade him (e.g., by diving) and to the difficulty of inducing him to follow a performing bird into the water and away from the nest. The Jacana (*Irediparra gallinacea*) (Hindwood, 1944) is an interesting exception. Many wading birds injury-feign but only a few conceal their eggs by placing material over them; most ducks cover their eggs (with down) and many injury-feign as well; the grebes (*Podicipidae*) most aquatic of the three groups, cover their eggs but do not injury-feign. Their nest-enemies are mainly other birds. Some birds, such as the Mallard (*Anas platyrhynchos*), Whistling Teal (*Dendrocygna javanica*) (Cairns, 1940) and even the Arctic Skua (Williamson, 1949) injury-feign on water and land. Such behaviour is most characteristic of species whose chicks are subject to attacks by terrestrial and aquatic predators.

(c) *The adaptive value of injury-feigning is greater when the nest is insubstantial or inconspicuous than when it is impenetrable or conspicuous.*

This principle is closely linked with those which we have been discussing but is concerned with the structure of the nest more than its situation, though, of course, the shape and structure of the nest are often determined, to lesser or greater extent, by its position. Thus, many ground-level nests are inconspicuous or insubstantial, or both. The inverse relationship between conspicuous nesting and injury-feigning is due to conspicuous nests often being in positions which non-avian predators find it difficult or impossible to reach. (In this connection conspicuous nests are to be understood either as structures which are readily visible or nests which are easily found owing to the coloration or movements of the owners). They are usually protected by their situation on islands or cliffs, (Alcidae) in tall trees (Ardeidae), or at the tips of branches (Icteridae). In general, elevated nests are more conspicuous than nests on ground level because the latter are normally

well hidden from predators with a low view-point, and the positions of the former are apt to be betrayed by the movements of the owners silhouetted against the sky. Moreover, there is more activity at the nests of birds with nidicolous young than at the nests, usually on the ground, of species with nidifugous chicks.

When the nest-material is sufficiently substantial to protect the contents, or the nest is so placed in a crevice that it is fortified by its surroundings injury-feigning is uncommon. It does not occur, or is very rare, among the kingfishers (Alcedinidae), woodpeckers (Picidae) swallows and martins (Hirundinidae) which nest in such protected places. Dr. A. F. Skutch (*in litt.*) confirms that in temperate and tropical America injury-feigning is rare in hole-nesting species and birds with elaborate or well-enclosed nests, such as wrens (Troglodytidae) and spine-tails (*Synallaxis*). Among cavity-nesting birds several factors protecting the nest, which may be said to operate in sequence, may have greater value than distraction display would have. The nest may (1) be in an inconspicuous situation and itself invisible, (2) be difficult of access, (3) have a restricted aperture, and (4) the birds may use forms of deterrent behaviour other than distraction display. Thus tits of many species when disturbed while incubating will flip their wings to make a puff-hiss sound (Pickens, 1928; Bent, 1946; Armstrong, 1947; Hinde, 1952)—behaviour which probably evolved where snakes were a menace. The Wryneck (*Jynx torquilla*) hisses and darts out its tongue like a snake (Coward, 1920). Motmots, such as (*Momotus lessonii*), sway their tails in such a manner as to deflect a predator's attention from the nest-burrow (Wagner, 1950, 1951).

The inverse relationship between injury-feigning and cavity-nesting is illustrated in the buntings. Distraction display of this type is characteristic of most, if not all, the Emberizidae of northern temperate regions and is particularly accentuated among those which nest on, or close to, the ground, especially the Lapland Bunting (*Calcarius lapponicus*). It has not been recorded of the Snow Bunting (*Plectrophenax nivalis*). Both are arctic species, but the Lapland Bunting breeds in the open while the Snow Bunting chooses rock crevices. The Snow Bunting's lack of an injury-feigning display is thus associated with the immunity of the nestlings from predation. They can be heard calling at a distance of 150 yards (Nicholson,

1930). Tinbergen (1939) has pointed out that such self-advertisement would be dysgenic if the chicks are accessible to predators. The noisiness of nestlings is often a measure of the safety of the nest. Young woodpeckers in the tropics, as in temperate regions, utter a sustained chorus but nestling Swallow Tanagers (*Tersina viridis*) in Venezuela do not call when the parents are away foraging (Schaefer, 1953). The nests of this species, in cavities in earth banks, are more accessible than the tree-trunk nurseries of woodpeckers.

As a rule cavity-nesting birds have a longer nestling period than open-nesting species and their success is greater (Lack, 1947-48). If injury-feigning were directly related to the duration of the nestling period we should expect it to be highly evolved among cavity-nesters. That it is not shows that the degree of exposure of eggs and chicks to predation is more important in this respect than the length of time which the young spend in the nest.

Certain exceptions to the rule that injury-feigning is rare among birds nesting in "fortified" nests or situations are of interest. Behaviour of this type is recorded of a number of tit species (Grimes, 1936; Odum, 1941-42; Hebard, 1949). Pettingill (1937a) describes an Acadian Chickadee (*Parus hudsonicus*) toppling over and hanging upside down from a branch when approached by a Red Squirrel (Cf. Wellman, 1938) and Hinde (1952) mentions a Great Tit (*P. major*) which rolled over on one side and held a wing up for some seconds. Hinde (personal communication) points out that the optimum releasing situation for this kind of behaviour is the cry of pain of the young. Such cries are usually uttered as the predator carries the chick away. Thus the distraction display in such instances appears to be relevant to a situation in which one or more of the young are out of the nest, rather than to the nest and its contents. As we have noted, in many species injury-simulation is most accentuated about the time when the young leave the nest, especially if they are alarmed or seized by a predator shortly after they have left. In such circumstances the adaptive value of the performance would consist in confusing the predator and deflecting his attack from the young to the adult. Distraction display may even be performed in response to the cry of pain of another species. A pair of Northern Yellowthroats (*Geothlypis trichas brachydactyla*) injury-feigned when a young fledged Cowbird (*Molothrus ater*) fostered

by them was captured (DuBois, 1953). It is doubtful, however, to what extent injury-feigning is effective in causing a marauder to relinquish a chick which he has already seized.

Such exceptions as those mentioned do not invalidate the rule, for it is adaptive that distraction display should be accentuated when it is likely to be most effective—and with many cavity-nesting birds and others this is when the young first quit the nest and are particularly vulnerable.

These considerations serve to call attention to an important general principle. The biological value of distraction display lies mainly in its effectiveness in attracting the attention of the predator before he has found the nest or is close upon the chicks. This is on account of predators' adaptations being such that they (1) concentrate on a nest once it has been found and are not easily deflected from it, and (2) are prone to return to a discovered nest or nesting colony to plunder it further (Armstrong, unpublished).

The inefficacy of distraction display in relation to marauders which concentrate on locating nests and are not predators in the usual sense of the term is shown by the extent to which Cowbirds victimise Parulidae which perform injury-feigning displays; sometimes over 50 per cent of nests contain a young Cowbird (Friedmann, 1929). These birds, and Cuckoos of a number of species (*Cuculidae*), find nests by persistently watching the birds themselves. If, as seems probable, birds do not injury-feign to brood-parasites, we may assume that this is due to the latter, not being carnivorous, having no inducement to follow apparently crippled birds.

Inconspicuous nests are generally in situations more accessible to ground and arboreal predators than conspicuous nests, and behaviour which deflects attention from them is therefore particularly valuable in, so to speak, giving the nest additional concealment by stimulating the predator to look elsewhere than the nest-site. Thus any odd, conspicuous behaviour may function defectively. To illustrate the close correlation between injury-feigning and inconspicuous types of nest on ground level it will be sufficient to mention the waders (*Charadriiformes*). Many make very meagre nests and all of them lay cryptic eggs. This correlation between injury-feigning and insubstantial nests appears to hold for a variety of types of nest site. Although, as we have noted, injury-

simulation is commoner among birds nesting on open terrain than in thick cover there are some injury-feigning species which nest low down in dense vegetation. The Reed Bunting and King Rail (*Rallus elegans*), (Meanley, 1953), frequently show such behaviour and the Water Rail (*R. aquaticus*) and Grasshopper Warbler (*Locustella naevia*) do so occasionally (Turner, 1924). These birds breed on ground level in dense and homogeneous vegetation where the nest is invisible until approached closely and the environment gives few or no clues to a predator as to the most profitable place to look. In this respect reed beds are comparable with tundra.

Among bush-nesting and injury-feigning birds a number make flimsy, small, or otherwise very inconspicuous nests—American Warblers, such as the Magnolia and Chestnut-sided (*D. pensylvanica*), antbirds (*Formicariidae*) which give distraction display more than any other group in the Central America lowland forest (Skutch, 1946; *in litt.*), the Shrike (*Nicator chloris*) of the African evergreen forest whose nest is a "lacy affair" (Moreau & Moreau, 1937), minivets in India (Dewar, 1928) and the Columbidae, the only group of almost world-wide distribution in which tree-nesting and injury-simulation are common (Dewar, 1928; Witherby *et al.* 1940; Skutch, 1946; Swarth, 1935; Allen, 1936; Hebard, 1949).*

(d) *Injury-feigning has most adaptive value among non-colonial birds.*

The vast majority of injury-feigning species

* Mayr (1946) regards the Columbiformes as of great age and Old World origin. He considers that the stock spread to South America in the Middle Tertiary. Their injury-feigning behaviour, flimsy nests and white, oval eggs, so unusual among tree-nesting birds with open nests, suggest that the Columbiformes may have evolved from a stock which originally nested in recesses on the ground. Perhaps the history of the order may have been similar in some respects to that of the Procellariiformes. The type may have evolved in actual or ecological islands, for the structural food-storage adaptation, whereby the parents can absent themselves from the young for a long time, foraging, if necessary, at a great distance, may have originally served a similar function to the food-retention adaptations of the Procellariiformes. Both groups produced large forms nesting on islands. The Fulmar (*Fulmarus glacialis*) emancipated itself from hole-nesting by evolving large size, the capacity to defend itself by squirting oil (Armstrong, 1951a) and cliff-ledge nesting. Some of the Columbidae are also well able to defend themselves (Dickens, 1953). A number of species, such as the Stock Dove (*Columba oenas*) (Walpole-Bond, 1940) and the Ground Dove (*Columbigallina passerina*) may nest either on the ground or in bushes.

breed in territories so large that the finding of a nest by a predator cannot facilitate the discovery of other nests—except, of course, in so far as experience may enable the animal to appreciate the kind of place to look for them. Of the many injury-feigning passerines none nests colonially.

The exceptions to this rule are of interest. They include Little Pratincoles (*Glareola lactea*), (Dewar, 1913), Pied Stilts (*Himantopus h. novaezelandiae*) (Guthrie-Smith, 1929), Avocets (*Avosetta recurvirostra*), Skimmers (*Rynchops albigollis* and *R. nigra*) (Dewar, 1928; Pettingill, 1937b), Sandgrouse, Black-bellied Terns (*Sterna melanogaster*) (Dewar, 1928; Worth, 1953), and Sooty Terns (*S. fuscata*) on Laysan (Fisher, 1906). The nests of all these are inconspicuous and their proximity to one another is apt to vary according to circumstances. Some nest on mud flats and in similar situations where the water level or restricted accommodation may force the birds to nest closer together than they would do if a larger area were available. All the conspicuous species in this category usually breed where water provides some protection from non-avian predators and some of them, such as the Avocet (Armstrong, 1925) and Black-bellied Tern are demonstrative against intruders, but their bills tend to be delicate as compared with those of many bolder colonial species and some have relatively fragile legs. Distraction display is a device whereby the relatively defenceless protect their nests by guile.

The social nesting of some of these large, conspicuous and apparently rather vulnerable species cannot be regarded as a recent adaptation (or maladaptation) for their white plumage and structural specialisation suggest that their social characteristics are of long standing (Armstrong, 1946).*

Where injury-feigning birds such as Piping Plover (*Charadrius melodus*) nest socially a number may perform simultaneously when an intruder appears (Robbins, 1919). Descriptions of such behaviour by Little and Grey Pratincoles (*Galachrysis cinerea*) (Seeböhm, 1885; Dewar,

1913, 1928; Brown, 1947) do not make it clear to what extent the corporate display may be mimetic (Armstrong, 1951b) rather than due to the effect of the intruder in releasing this behaviour in each individual.

Williamson (1949) remarks that as many as five Arctic Skuas may be seen injury-feigning 30 or 40 yards from the observer. He considers that the birds mutually stimulate each other. Conclusive evidence of mimetic injury-feigning is provided by an observation of a Shoveler (*Spatula clypeata*) which settled near an injury-feigning Mallard and displayed in the same way (Hickling, 1950). Chisholm (1948) mentions communal distraction display by White-fronted Chats and Yellow-tufted Honeyeaters (*Meliphaga melanops*). Mr. P. Bourke (*in litt.*) remarks that he has seen such performances by the Yellow-tufted and White-cheeked Honeyeaters (*Meliornis niger*): "In both cases other individuals in the vicinity join in and you may have three or even more displaying around you at once." Such social displays may have arisen as an outcome of the curiosity which stimulates birds to investigate a commotion in their neighbourhood. This response may have selective value, as birds are seldom captured by a predator to whose presence they have been alerted. Probably in some instances, the utterances of the injury-feigning bird may attract others. Grimes (1936) states that sometimes a neighbour or two may flutter around a displaying Hooded Warbler (*Wilsonia citrina*) and Wetmore (1920) refers to males other than the bird's mate flying down towards an injury-feigning White-winged Dove (*Zenaida asiatica*). Ditmars (1946) remarks that on more than one occasion he has been attracted to where a bird was decoying a snake from the nest by the scolding notes of other birds watching the performance from nearby trees. In Cuba a flock of Groove-billed Ani (*Crotophaga ani*) will crowd excitedly around a dove when it injury-feigns (Davis, 1940, 1942). Some types of this behaviour, which have affinities with mobbing, may be adaptive, for a predator would probably be more bewildered by several displaying birds than by one. If so, the relaxation of territorialism is sometimes advantageous. In so far as territorialism is related to predation (Tinbergen, 1952b) a species has to reach a compromise between the concealment afforded by isolation and the protection attainable by corporate aggressive or deflective activities.

Birds seldom injury-feign to an individual of

* Certain generalisations may be made in regard to the morphology of injury-feigning birds but in a primarily ecological paper they can only be mentioned. Thus, injury-simulation is rare or unknown among very small birds, such as the Humming birds (*Trochilidae*) and Sunbirds (*Nectariniidae*). It is also rare among brilliantly plumaged or extravagantly adorned birds. This may be partly correlated with the cavity-nesting of many species. It tends to be poorly developed among powerful and strongly armed birds.

their own species, but Williamson (1948) flushed a Golden Plover (*Charadrius apricarius*) which went off with "impeded flight" and then injury-feigned to its mate. Apparently this was a form of "transference activity"—behaviour in which a drive is expressed in relation to an inappropriate object (Armstrong, 1952a). The rarity of intra-specific injury-simulation may be due to the infrequency of the occasions when a bird attempts to plunder a nest of its own species in circumstances when deflection display could be effective. Instances have been recorded of male birds reacting to their mate's distraction display by attempted copulation. In some species a wide range of objects may elicit distraction display (Cf. Appendix).

(e) *Distraction display has adaptive value in proportion to the extent of jeopardy from diurnal predation.*

Earlier comments have stressed that elaborate distraction displays presuppose posturing which is clearly visible to the marauder. Darkness nullifies the effect of such posturing so that the search for the creatures responsible for their evolution and maintenance may be concentrated almost entirely on diurnal predators. Injury-feigning by the Nightjar (*Caprimulgus europaeus*) is less accentuated in the evening (Lack, 1932) and at night it gives a threat display (Stülcken & Brull, 1938). Deane (1948) noted that an "American Nightjar" in Ontario injury-feigned to him by day but threatened a cat at night. Although injury-simulation is widespread among the Caprimulgidae it is not recorded of the Guacharo or Oil Bird (*Steatornis caripensis*) which nests in completely dark caverns.

In some regions, especially in deserts and in the tropics where only a small percentage of terrestrial nest-predators are diurnal, the field of search is thus greatly contracted. Even within this field the possibilities can be still further reduced by the elimination of almost all of the most numerous group, namely, avian predators. It is improbable that they have exercised a significant influence on the evolution of injury-feigning displays. Instances of one bird performing distraction display to a major avian predator of the species are rare, probably because an injury-feigning bird would be vulnerable in such circumstances.

Brown (1947) saw a Pied Crow (*Corvus albus*) leisurely pick up an egg from the nest of Egyptian Plovers (*Pluvianus aegyptius*) while the owners "were shuffling about in the sand, trying their

hardest to draw off the crow." A Red-shouldered Hawk (*Buteo lineatus*) apparently was prevented from seizing Wood Duck (*Aix sponsa*) ducklings by the "broken-wing" behaviour of the parent (Saunders, 1937) but a Dotterel displayed uselessly to a Rough-legged Buzzard (*Buteo lagopus*) after the young had flown away (Haviland, 1917). Other instances are: Long-tailed Duck (*Clangula hyemalis*) to Red-throated Diver (Nicholson, 1939), Mallard to Mute Swan (*Cygnus olor*) (Armstrong, 1953), Canada Goose (*Branta canadensis*) to Mute Swan (Tennent, 1948), Kentish Plover (*Charadrius alexandrinus*) to Ringed Plover (Selous, 1927), Little Ringed Plover to Ringed Plover (Armstrong, 1952b), and Lapwing (*Vanellus vanellus*) to Pheasant (*Phasianus colchicus*) (Spencer, 1953). The only species in this list known to be a persistent predator on the species it was seen menacing is the Pied Crow—and the parents' antics were futile. It is improbable that either of the two *Buteo* species is a major enemy of the birds they were seen alarming.

We are left with reptiles and mammals as the animals primarily responsible for the origin and maintenance of injury-feigning, but we must be wary of assuming that the animals now found in the habitats of injury-feigning birds are responsible for the peculiarities of these displays. The "broken-wing" behaviour of the Galapagos Ground Dove (*Nesopelia galapagoensis*) must be a survival of the behaviour of birds which reached the islands very long ago. The species has been established long enough to have diverged into two distinct races (Swarth, 1931) yet injury-feigning continues although there is no animal on the Galapagos to persecute it. Kerguelen Teal (*Querquedula eatoni*) (Moseley 1879) and the Sooty Terns on Laysan (Fisher, 1906) perform although they are not menaced by any indigenous predator. In some groups the very similar or identical distraction displays of birds in widely separated areas shows that it would be unwise to attribute the displays to the selective effect of particular predators. Thus a description of the distraction behaviour of Jerdon's Little Ringed Plover (*Charadrius dubius jerdoni*) in India (Eates, 1937) might equally apply to the posturing of *C. d. curonicus* as I have seen it in Suffolk (1952b). On what seems too slender evidence Simmons (1952) has claimed a difference between the distraction display of the Ringed Plover in Europe (*Charadrius hiaticula*) and the Semipalmated Plover (*C. h. semipalmatus*) in Arctic Canada. The fact

that one can generalise in regard to genera, as, for example, that injury-simulation is much more accentuated in *Charadrius* than in *Tringa*, suggests that divergences in structure, nesting-habitat and predator reactions have often remained closely integrated.

That injury-feigning (as distinct from thanatophany) is practically non-existent in other groups than birds must be largely because its biological value is greatly reduced if the decoy cannot quickly escape into another element out of reach of the predator. The animals responsible for the evolution and maintenance of injury-simulation are practically limited to fairly small, diurnal, carnivorous, quadrupedal ground and arboreal predators, and some diurnal snakes.

Probably until long after the birds began their evolution from reptilian stock their main predators were reptilian. In this connection it is interesting to note that the Egg-eating Snake (*Dasyptis scabra*) is highly specialised to feed on eggs. As many early reptiles were quick-sighted, like modern lizards, it is not unlikely that injury-feigning, which does not occur among reptiles, may have arisen from their attacks. Evidence already cited indicates the importance of reptiles as bird-predators in North America. Dr. Skutch writes from Central America that he considers snakes the most important nest-predators and Mr. R. E. Moreau (*in litt.*) with wide experience in Africa thinks that snakes and monkeys are the worst enemies of nesting birds, with squirrels next in order. In Australia, where many birds perform distraction display (Boehm, 1946) most ornithologists regard reptiles, especially lizards, of which there are over 200 species, as important nest-predators. (For photographs of lizards at nests and the bower of the Satin Bower Bird (*Ptilonorhynchus violaceus*) see papers by Serventy, (1953), and Chaffer (1945)). Descriptions, such as Chisholm's (1948), of birds injury-feigning from trees suggest a small agile marauder, such as a lizard. The marsupials do not seem to have evolved efficiency as diurnal, arboreal predators comparable with some placental mammals and perhaps in so far as lizards are such destructive nest-robbers in Australasia bird-predation there still possesses some comparatively primitive characteristics.

In spite of difficulties and pitfalls some progress may be made, as our discussion of the behaviour of American warblers has shown, in identifying the predators most likely to have

exercised a selective effect on the evolution of the distraction displays of some groups. Sometimes we may even make inferences in regard to the past, aided by the knowledge that the adaptation of predator and prey must have proceeded *pari passu*.

In mid-temperate Europe, for example, the Mustelidae, especially the Stoat (*Mustela erminea*), and the Fox, may have played an important part in the evolution of distraction displays. The Stoat has a wide distribution, and in Britain followed the retreating ice more closely than the Weasel (*M. nivalis*), as the absence of that animal from Ireland indicates. It is probably the most diurnal of the European Mustelidae, swims readily and climbs expertly. Its depredations among birds are notorious. It will raid the nests of passerines and ducks (Baker, 1914) or snatch a chick from under a pheasant as I have seen one do. Middleton (1935) found that Stoats were responsible for 1.9 per cent of Partridge (*Perdix perdix*) nests destroyed. Lynes (1910) saw a Stoat being lured 400 yards by an injury-feigning Lapwing. The Weasel also can be a serious menace to nesting birds. Male (1950) watched a female Blackcap enter a thicket to her unlined nest. Almost immediately a Weasel emerged holding the bird in its mouth. The cock attacked the animal seven times as it carried his mate away; then he fluttered ahead with wings outspread for 25 or 30 yards.

Southern & Watson (1941) record that small birds come next after Rabbit and Sheep in the Fox's summer diet. Before these animals were introduced the Fox may have hunted birds even more seriously. The predatory habits of other mid-temperate mammals, such as the Wild Cat (*Felis sylvestris*), the Badger (*Meles meles*) and the Hedgehog (*Erinaceus europaeus*) suggest that their ravages have been of subsidiary importance in this regard.

One can speak with more confidence of the relevant predators in the sub-arctic and arctic than elsewhere, for reptiles need not be considered and the number of small predatory mammals is very limited. No doubt the Mustelidae have influenced distraction display in parts of this circumpolar belt, but undoubtedly the Arctic Fox is, and has long been, the chief, and in some areas, the only non-avian bird predator. Moreover, the distraction displays of several high northern birds appear to owe their specific characteristics to the selective effect of its attacks. Most noteworthy is the so-called

"rodent-run" of the Purple Sandpiper (*Calidris maritima*). Retreating from the nest it humps its body, shuffles its wings and runs in a zig-zag fashion (Witherby *et al.*, 1940; Duffey & Creasey, 1950). All observers agree that the resemblance to a small mammal is striking. Jourdain (1936) was confident that the performance would deceive the Arctic Fox, and Duffey & Sergeant (1950) consider its display "an important factor in enabling it to maintain its numbers" on fox-infested Bear Island. The Sanderling (*Crocethia alba*) and Dotterel, both birds of the high north, also act in a way suggestive of a small mammal. (Manniche, 1910; Witherby *et al.*, 1940). Descriptions of the behaviour of the Knot (*Calidris canutus*) (Witherby *et al.*, 1940) suggest somewhat similar behaviour. Scott (1951-52) noticed a Dunlin (*Calidris alpina*) running like a small rodent and squealing like a rat, the dark line down the middle of the spread tail suggesting a mammal's tail. I have seen Golden Plover performing the rodent-run and Ringed and Little Ringed Plover doing a crouch-run somewhat resembling it. Williamson (1950) and Blair (1950), cite a number of other species with a northerly distribution which behave in a similar way.

Several aspects of this type of display deserve emphasis. Apparently it is the main or only distraction display performed by the Purple Sandpiper—a bird of high northern latitudes—and it is most prominent among species whose range extends into the Arctic Fox's area of distribution. We must assume that the display evolved where the Arctic Fox, birds and small rodents occurred together—probably in continental Northern Eurasia and not among the great islands of the north where rodents are few or do not occur. After the periods of extreme glaciation when the birds and the Fox were pushed southward some species with rodent-run behaviour such as the Dotterel and Golden Plover, held their ground in Britain.

This argument is not impaired by the evidence of somewhat similar behaviour by passerines in other regions. Littlejohns and Lawrence (1920), Chaffer (1923, 1929), Chisholm (1950) and others have drawn attention to the "mouse-like" behaviour of Australian members of the genus *Malurus* but it is not clear that the movements mimic those of any endemic member of the fauna. Snakes have been seen capturing these birds (Elford, 1953), Roberts (1944) refers to forms of distraction display by them as "illness-feigning." Such behaviour has been

recorded of Emu Wrens (*Stipiturus malachurus*). Better evidence of mimicry is furnished by Allen (1951), referring to the Green-tailed Towhee (*Chlorura chlorura*) in the Great Basin of western North America. It nests in sagebrush (*Artemisia*) a foot or two from the ground and, when flushed, drops to the ground. Its appearance and movements as it runs off conspire to create a close resemblance to a Chipmunk (*Eutamias*). Allen believes that Coyotes (*Canis latrans*) are deceived by this performance. It is not surprising that birds of the high arctic and this quasi-desert area should show convergent behaviour in reference to predators so similar in many respects. The open alley-ways in the brushwood offer a setting for the display corresponding to tundra. The light is strong, and even at night the moonlight is sometimes so brilliant that a Coyote would probably be able to distinguish details of the movements of the bird over the sandy ground.

(f) *Injury-feigning has greatest adaptive value in northern latitudes.*

This principle is mainly a corollary of that just discussed because in high latitudes all predation during the height of the birds' breeding season is diurnal. Continuous summer daylight and wide visibility in areas beyond the tree-limit create conditions in which distraction display might be expected to be, and apparently is, of maximum advantage. It is very common and has been recorded of arctic and sub-arctic birds belonging to the following families: Colymbidae, Anatidae, Falconidae, Tetraonidae, Balaeridae, Haematopodidae, Charadriidae, Scolopacidae, Phalaropodidae, Stercorariidae and Strigidae, as well as of a number of families of the Passeriformes. Indeed, beyond the tree-zone it is exceptional for any species not usually nesting on cliffs or islands to be without a form of distraction display.

My own experience in the Asian and American tropics, as well as the views of correspondents, indicate that injury-feigning is relatively uncommon in these latitudes. Edgar (1947), mentioning the distraction display of the Malay Pipit (*Anthus novaeseelandiae malayensis*), remarks, "Not many birds in Malaya seem to feign injury."

It would be an interesting confirmation of a direct correlation between length of daylight and injury-feigning if it could be shown that there is in any species a cline in accentuation northwards. Convincing evidence is necessarily

difficult to obtain because observers may assess the vigour of display differently. The evidence available is quoted for what it is worth.

Distraction display is not common in the southern race of the Golden Plover (Nethersole-Thompson, 1904a) but Williamson (1948) noted it frequently in the Faeroes and Dr. F. Gudmundsson tells me (*in litt.*) that the Golden Plover in Iceland "always shows an elaborate injury-feigning at the nest if the eggs are incubated." Williamson (1950a) also brings evidence suggesting that such display is more frequently performed by the Snipe (*Capella gallinago*) in the Faeroes than in Britain. A bird, excited by my presence near the young in Lapland, performed mild distraction display.

Williamson (1943) has shown that in the Faeroes the Oystercatcher (*Haematopus ostralegus*) exhibits comparatively elaborate distraction displays. He maintains (1952) that on Unst and Fair Isle the displays are less accentuated than in the Faeroes but more developed than in southern Britain and the continent, and this is borne out by my own experience, so far as Shetland and areas to the south are concerned. Makkink (1942) describes only mild displays by Dutch Oystercatchers. However, information from Dr. Gudmundsson does not indicate that highly evolved display occurs in Iceland. Williamson believes that in the Faeroes the accentuation of distraction display is due to "the psychological effect of frequent disturbance of the brooding urge by man, during the attempt to colonise a new and unsympathetic environment." This view is open to the objection that in other places where the Oystercatcher breeds away from the seashore and is liable to much human disturbance, as in Holland, it has not evolved distraction displays comparable in variety and vigour to those of the Faeroe birds. It is also difficult to believe that man has played a predominant role in the evolution of these displays, for the Faeroes were not colonised until the eighth century A.D., and as Williamson points out, the Oystercatcher has had "the revered status of a national emblem" for a century. Simmons (1952) believes that the influence of man as a selective agent on distraction display has been under-estimated but this is improbable. Apart from other considerations human population before the Bronze Age and for the most part during it, was too sparse, except in a few tiny regions of Asia, for man to have exerted any appreciable influence. There are a few instances of humans being temporarily

tricked by injury-feigning birds (Feilden, 1872) but it is very unlikely that efficient hunting people, such as the Magdalenians, could have been frequently duped by injury-feigning birds.

It is evidence in favour of a cline northwards in the accentuation of distraction display, due to extended summer daylight, that such accentuation should occur in the Faeroes and parts of Shetland where there are no relevant indigenous predators to exercise a selective influence. However, it must be remembered that birds of unfrequented places tend to be bolder—some would call them "tamer"—than birds of thickly populated regions. There is a tendency for boldness and vigorous injury-feigning to be associated. This supports the view that distraction display is the product of the clash of the drive to escape and parental protective impulses but it raises the problem, only to be solved by experiment, of why some birds rapidly become conditioned to human intrusion so that they cannot be made to injury-feign, whereas others continue to perform however often trials are made (Armstrong, 1950), (Cf. Appendix).

Study of distraction display in the light of this and other principles enumerated may furnish clues in regard to the evolutionary history of species and larger groups. Thus injury-simulation is characteristic of the Arctic and Long-tailed Skuas (*Stercorarius longicaudus*) but not of the two larger species, the Pomarine and Great Skuas (*S. pomarinus* and *S. skua*). Although forms of the latter are found in the antarctic we can conclude that the Skuas did not originate there because (1) all four species are found in the arctic, (2) the two smaller species injury-feign, and as ground predators on birds are practically non-existent in Antarctica injury-feigning is almost unknown there, and (3) in the antarctic the chicks of the Great Skua tend to disperse from the nest when disturbed as they do in the arctic. This adaptation must be valuable where there are ground predators but is apt to be dysgenic in a region of bird predators, such as the antarctic. Thus the Great Skua's lack of injury-feigning is correlated with its large size and aggressive habits and not with an origin in Antarctica.

The distribution of the Turnstone (*Arenaria interpres*) presents an interesting problem. It breeds around the Arctic Ocean and as far south as Sweden and the southern coasts of Alaska and Kamchatka, and also in the neighbourhood of the Caspian and Aral Seas. Brandt (1929),

Sutton (1932) and Hebard (1949) agree that *Arenaria i. morinella* does not injury-feign and Bergman (1946) who intensively studied *Arenaria i. interpres* does not mention behaviour of this kind. Although Manniche (1910) refers to a female in Greenland which by "anxiously flapping tried to direct attention" from the fledged young, it seems that distraction display is almost, if not quite, non-existent in this species. May it be a bird of southern origin which colonised the north after the Ice Age, leaving a population in the Caspian area? Its choice of nesting-place in Finland and Southern Sweden among herbage or concealed in rock clefts suggests that it is not essentially a tundra species. The only other birds with similar breeding behaviour are species of arid habitats which, in seeking prey, displace cakes of dried mud (Jaeger, 1950). Thus it should not be assumed that the Turnstone necessarily acquired its peculiar feeding adaptation in a northern littoral area.

Appendix. The Characteristics of the Objects Releasing Injury-simulation Behaviour

In most species there are wide limits to the types of object which elicit injury-feigning. Thus a Spectacled Warbler will display to a snake or a cat (Gibb, 1947) and a Mallard to a bird of prey, a Swan (*Cygnus olor*), an Otter (*Lutra lutra*) (Pitt, 1927) or a man. Observation suggests that birds of this species sometimes start to injury-feign before they perceive the nature of the intruder so that the reaction may be a surprise-response to any sufficiently startling occurrence close to the brooding bird. In other species, too, the reaction may be generalised but the object eliciting the behaviour need not necessarily appear suddenly or be mobile. A Stone Curlew displayed to a dog (Woodward, 1938) and another to a photographer's hide (Yeates, 1936). When a Merlin (*Falco columbarius*) caught sight of a camera lens protruding from a hide it began "to flop about with extended pinions over the heather in a way strongly suggestive of the antics a Teal had just employed" (Kearton, 1903). A Ringed Plover performed distraction display on seeing artificial eggs placed on the edge of the nest (Koehler & Zagarus, 1937).

On the other hand some species react differently to different kinds of objects. Pintails (*Anas acuta*) perform when alarmed by a ground predator but not when a Harrier (*Circus sp.*) passes over (Hochbaum, 1944). The Killdeer

flies up at the head of a horse or cow but injury-feigns if a man or a dog approaches (Taverner, 1936; Deane, 1944). Lacey (1911) saw one of these birds force an advancing herd of goats to divide and pass its nest by standing over it with wings outspread, scolding vigorously. When Skinner (1929) approached Killdeer's nests on horseback the brooding birds first stood in threat display with wings spread and then injury-feigned. (Lord Lilford (1929) found that in Tunisia he could not get within shot of Dotterel when on foot but that they could be closely approached when he was mounted on a horse, donkey or camel). According to Spencer (1953) Lapwings are particularly prone to injury-feign to people on bicycles (Cf. Nethersole-Thompson, 1940b). Perhaps this is due to the surprise caused by the rapid approach of cyclists. One of these birds feigned injury to a sheep after trying to deter it by threats and assaults (Nethersole-Thompson, 1940b). The Spur-winged Plover (*Lobibyx novae-hollandiae*) and Black-breasted Plover (*Zonifer bicolor*) perform distraction display to people but attack quadrupeds (Campbell, 1901; Chaffer, 1944). A Black-winged Stilt gave a distraction display before a flock of sheep but threatened a newborn kid (Nice, 1943). A Texas Nighthawk (*Chordeiles acutipennis texensis*) injury-feigned to an erect man but when he approached on all fours assumed its most cryptic appearance, then threatened, and finally injury-feigned (Pickwell & Smith, 1938). All these birds nest in situations where they are able to observe the characteristics of an intruder before he is close to the nest. These examples confirm the view that injury-simulation is apt to occur when the escape drive dominates the drive to defend eggs or young. This is further illustrated by instances, such as occur among Pratincoles (*Stiltia isabella*) when the female remains on the nest and pecks the intruder while the male injury-feigns (Campbell, 1901).

Few experiments on distraction display have been made. Howard (1929), using a Ferret (*Putorius furo*) at the nest of a Reed Bunting, decided that it was the suddenness more than the strangeness of the stimulus which elicited the response. This agrees with the opinion expressed above regarding the Mallard's displays. The Buntings perched, calling, with tails spread, as they do on seeing a Stoat or a Weasel approach the young, except when the Ferret was thrown just beside the nest, or when Howard stood up suddenly when the female

was perched above the Ferret. In the latter instance the combination of the two strange objects may have been particularly stimulating as one would expect according to the law of heterogeneous summation (Seitz, 1941) (Cf. Edwards *et al.* 1947 for another example). Similarly, a Blackcap (*Sylvia atricapilla*) which had been watching and calling at a cat injury-feigned when I appeared.

In contrast, birds which become familiar with an object to which they would normally injury-feign may not then do so. Lorenz (1935) found that tame birds would not display to him. Berg (1925) tamed a Dotterel so that instead of injury-feigning to him it would sit brooding its eggs in his hand while he fed it with worms. Goodwin (1953) found that the distraction displays of a Red-legged Partridge in an aviary decreased in vigour. The Talpacoti Ground Dove (*Columbigallina talpacoti*) is an injury-feigning species but when Haverschmidt (1953) visited a nest daily he was able to lift out the young without the parent doing more than raise a wing. On the other hand I accustomed a Ringed Plover to my presence so that if I approached slowly I could place my fingers under its breast as it brooded but I could always elicit injury-feigning by alarming it slightly. Pitt (1927) had a tame duck which would not perform to her but did so vigorously when an Otter approached. A Nightjar will continue injury-feigning for a long time if the intruder remains by the nest but it does not react in this way on returning after once having flown away (Lack, 1932).

Thus among the characteristics of a situation releasing injury-simulation the most typical and generalised appear to be (1) abruptness of the stimulus, (2) movement, especially advancing, and (3) the characteristics of a customary predator or unfamiliarity of appearance. A bird seldom injury-feigns to an object smaller than itself but the instances cited above show that there cannot be assumed to be a direct relationship between large size and the degree of stimulus to injury-feign.

Systematic observation and experiment are needed to determine the relationship of the factors which operate in eliciting distraction display and the extent to which innate mechanisms, habituation, conditioning and learning determine such behaviour.

Summary

1. Injury-simulation displays are considered

to be due to the conflict between impulses associated with the defence of nest and eggs or young and the escape drive.

2. Principles correlating the incidence of distraction displays and the type of nesting habitat are formulated. It is suggested that injury-simulation is most adaptive for species with relatively inconspicuous nests in vulnerable situations primarily exposed to diurnal ground predators.

3. Evidence is cited indicating the types of predator most likely to have been responsible for the evolution of certain forms of distraction display in specific habitats.

4. It is suggested that the distraction displays of species and groups may, in some instances, throw light on their evolutionary history.

5. The principal factors releasing injury-simulation behaviour are considered.

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ADDENDUM

THE DISTRACTION DISPLAYS OF THE BLACK-WINGED STILT

Since this paper was written I have been able to study the distraction behaviour of the Black-winged Stilt. Except for brief notes in the papers cited above there appear to be no descriptions of these displays apart from a few lines in papers by N. Binsbergen and J. P. Strijbos in *Thijssse-Gedenkboek* (1935) and J. E. Sluiter in *Orgaan Club. Ned. Vogelk.*, 1935, **8**, 11-12). During the low-intensity display the bird stands waving its wings, only partially raised and spread, more or less vigorously. Flapping birds commonly raise one wing higher than the other and may make little lurching runs through the *Salicornia* clumps so that they are partially concealed. Displacement-brooding sometimes occurs. When excitement increases the flapping becomes more energetic so that the birds become air-borne and mount some six feet or more. The wing-waving on the ground and the vertical flights,

which are accompanied by loud "kweeuk" calls, may be performed by a number of birds simultaneously, dotted here and there over the breeding ground, often fifty yards or more from the intruder. The displays give the impression of a compromise between the impulse to flee and the impulse to remain near the young and demonstrate against the intruder. Their effectiveness would seem to lie more in their being such as to attract the attention of predators at a distance than in mimicking injury. Indeed the distance at which Stilts often display would appear to preclude appreciation by predators of the finer details of realistic injury-feigning such as is performed by the Killdeer and Ringed Plover. None of the displays appeared to be mimetically induced. Further details will be published elsewhere.

E.A.A.

Finding and Exploitation of Dishes of Syrup by Bees and Wasps

By H. KALMUS

University College, London

Interest in the study of the behaviour of the various social hymenoptera is at present reviving and much knowledge is being added to the classical observations of Lubbock (1882). The following is a comparison of the way in which two social Hymenoptera, *Apis mellifica* L. and *Vespa germanica* F. exploit a new source of food.

Period Elapsing Before Detection of the Feeding Site

In August, 1952, a colony of some 40,000 Buckfast strain bees which had not been previously fed on Petri dishes was moved into a garden some distance away from any other hive. No wasp's nests were found in the immediate neighbourhood. On the next day, when many of the workers were flying in the garden, a glass-topped table on which there were 4 Petri dishes containing 67 per cent. sugar syrup was set up about 25 yards from the bee hive. After 92 seconds a wasp searched the table, and after a further 14 seconds it started feeding on the syrup in one of the dishes. It was daubed blue on the thorax and was observed to return to the same dish four times. Three minutes, forty-eight seconds from the beginning of the experiment another wasp alighted on another dish; this second wasp was daubed red but was never seen again. For the next 5 hours varying numbers of wasps (0—6) were observed on the dishes but no honey bee paid them any attention although many were flying in the neighbourhood. Four hours sixteen minutes after the dishes had been put up the first honey bee hovered over the table, and about a minute later she settled and was marked. After she had returned three times, other bees, presumably alarmed by her (v. Frisch, 1946), began to arrive in the neighbourhood and soon the number of visitors mounted. Ten minutes after the first arrival of the first bee, three other bees were simultaneously drinking on the same dish; after fifteen minutes nine bees were drinking on three of the four dishes and after twenty-nine minutes a cluster (Kalmus, 1953) of about 200 bees had formed on the first visited dish, which

then quickly dried up. While the number of honey bees quickly rose, the number of visiting wasps remained very much the same as before, and never rose to more than eight at the same time.

Similar observations were made at the beginning of other experimental series, when single syrup dishes laid out in the vicinity of untrained bees remained undiscovered for 4 hours 32 minutes, 6 hours 50 minutes and 27 hours 12 minutes (overnight), while in every case wasps found the dish after a few minutes. A long delay in the detection by honey bees of a new kind of food is well known (v. Frisch, 1919), and the rapidity of wasps in finding and exploiting it is very striking. Under natural conditions the vast majority of bee foragers are usually attached to a particular crop, whereas only a small minority search for new sources of food. Searching and collecting are not rigidly separated activities; they may occur in the same worker bee; Oettingen-Spielberg (1949) considers that the searching activities of wasps must be similar to the behaviour of searching bees and that the more conspicuous behaviour of the many collecting bees obscures this similarity. One must, however, assume that between searching wasps and searching bees there are considerable behaviour differences, which are founded in the difference of their sense organs and innate preferences. The fact remains that in spite of the presence of 40,000 worker bees 25 yards from the feeding site, and the absence of any wasp's nests in a radius of at least 60 yards, more wasps were probably searching in the area than bees.

Detection of the Site by Wasps in the Area

The ability of wasps quickly to discover a group of syrup dishes was used to provide a rough estimate of the wasps foraging in that neighbourhood. For this purpose all the wasps which settled on the training table when it was put out for the first time were caught and removed, and the time of their arrival was recorded. A few wasps escaped and that fact was also recorded. It is very likely that these

TABLE I. Number of *Vespa germanica* Captured on 4 Freshly Laid Out Dishes Containing Dilute Syrup, in the Absence (top) and Presence (bottom) of Honey Bees.

Period in minutes	<5	5-10	10-15	15-20	20-30	30-40	40-50	50-60
No. honey bees on dishes	12(2)*	9(1)	3	3	1	2	1	1
5-16 honey bees on dishes	4(2)	6(2)	4	5(1)	9	—	1	—

* () indicates wasps which escaped

returned and were then caught again. Two such observations made at different sites are presented in Table I; in one observation no collecting bees were tolerated on the site during the period reported; in the second observation between 5 and 16 bees were simultaneously present. In both experiments observation was interrupted half an hour after the last wasp arrived, and it was assumed that the number of wasps in the area was then exhausted. However, returning to the site after a further hour, four more wasps were caught on the dishes during a few minutes on the first occasion, and one wasp on the second occasion. After the counts the wasps were marked red and released some 50 yards from the feeding table and on both occasions many of them were feeding on the dishes after a few minutes.

In the first experiment 74 per cent. of the

wasps were obtained within 30 minutes, and in the second experiment, in which bees were present, 84 per cent. came in that time. Apparently the presence or absence of honey bees had no great influence on the numbers of wasps visiting the table. Only very occasionally did a bee attack a wasp, but the wasps were often aggressive and frequently pounced on drinking bees, making them fall into the syrup.

Constancy of Wasps

The constancy of collecting bees in respect of flower species and locality is well known, although it has on occasion been somewhat exaggerated, but searching bees cannot be constant. Observations summarised in Table II show that wasps were less regular in their visiting habits than trained collecting bees; they were also more easily disturbed and more difficult

TABLE II. Successive Visits to Four Dishes (1-4) Containing Dilute Syrup by Two Marked Wasps and Two Marked Honey Bees at the Beginning of the Experiment and After One Hour's Feeding

		No. of dish																		
Early visits	1st wasp	2, 3, 1*, 2, 1*, 4, 1, 4*, 4, 1, 3, 3, 1, 4*, 4, 1, 1, 3, 2, 1, 2, 1, 3, 4*, 3, 1*, 1*, 1, 4, 1, 3, 3, 4, 1,																		
	2nd wasp	2, 3, 1, 2, 3, 4, 1, 4*, 2*, 4*, 2, 4*, 4, 2, 4, 3, 1, 3, 1, 2, 4, 3*, 3*, 3, 1, 3, 4, 2*, 2, 1, 4,																		
	1st bee	1, 1, 2, 3*, 1, 1, 1, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, 3*, 3, 1, 1, 1, 1, 1, 1, 1, 3*, 1, 1, 1, 1,																		
	2nd bee	3, 3*, 3, 1, 3, 3, 3, 3, 2, 3, 3, 2*, 3, 2, 1, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3,																		
Visits after one hour	1st wasp	1, 2, 2*, 2, 2, 2, 2, 2, 3, 1*, 3, 1, 1, 2, 3, 2, 2, 2, 2, 1, 4, 1, 1*, 2, 2*, 2, 2, 3, 2, 2, 2, 2, 2,																		
	2nd wasp	2, 1, 2, 3, 1, 4, 3, 4, 4*, 4*, 4, 2, 4*, 4, 4, 4, 4, 1, 4, 4, 4, 4, 3*, 2, 1, 4, 4, 4, 4, 4, 4, 4, 4,																		
	1st bee	Seven visits at No. 1, then visit at No. 2, then 11 visits at No. 1.																		
	Another bee	Eighteen visits at No. 4																		

* short touch down—under 10 seconds.

to catch or mark than bee foragers. The figures in Table II show that successive visits by the two freshly arrived wasps were almost independent events so far as the probability goes that a particular dish would be preferred. Even after an hour the wasps were far less constant than the bees.

Differences in the Reaction of Bees and Wasps to Transitory Changes

Wasps were much less sensitive to transitory changes than honey bees. Their visits did not greatly change with alteration in syrup concentration nor with the weather. While an increase in syrup concentration quickly increased the numbers of visiting honey bees, the number of visiting wasps hardly changed. In one experiment replacement of 10 per cent. sugar syrup by 60 per cent. increased the number of bees on the dish within half an hour from an average of 8 bees to more than 10; at the same time the number of wasps on the dish remained between 1 and 4. This suggests that, unlike bees, wasps do not alert their colony mates.

On the other hand, wasps persisted much longer in collecting dilute syrup, and after rain they were observed to collect almost pure rain-water. When an empty and freshly washed dish was substituted for one visited by bees and wasps, the latter were put out for a far shorter time than the bees. When a drop of syrup was subsequently put into the empty dish, the one or two wasps near the dish settled down immediately, while for a minute not one of about a hundred bees settled. The bees may have been put off by the lack of their familiar body odour (Kalmus & Ribbands, 1952), whereas it seems that wasps do not scent a dish. Some wasps also collected during rain; their insensitivity to sudden change in weather and even to heavy rain contrasted with the hurried return to the hive of most of the bees when a cloud obscured the sun (Lundie, 1925), and their complete cessation of foraging during rainfall. On one occasion a heavy shower drove away all of 200 bees from the syrup dishes, while 6 wasps persisted in visiting them for at least 10 minutes; then the wasps disappeared too and 3 bees were seen near the dish during their absence; when the sun returned the first visitors were four wasps, and the first bee arrived four and a half minutes after the first wasp. This relative insensitivity of *Vespa germanica* to bad weather agrees well with similar observations on the North American *Dolichovespula arenaria* (Gaul, 1952). Bumble bees also collect during rain.

Discussion

The above observations illustrate correlations which exist in the hymenoptera between individual properties and social organisation. They also furnish a common yardstick for quantities usually considered to be incommensurate—for such diverse characteristics as individual acuity of perception or alertness on the one hand and division of labour and communication on the other hand. While the less complicated wasp society consists of hardier and more alert individuals which are always prepared to try something new, the more highly integrated honey bee colony compensates for inferiority in these respects by their greater numbers, ability to communicate, and the constancy of the behaviour of the majority of the collectors. While wasps are thus eminently suitable to exploit an environment offering a wide variety of food, even if each is only present in limited quantities, honey bees are better adapted to the presence of a few but abundant and widespread sources of nectar and pollen as occurs in certain natural and most man made environments. A small isolated source of food will be quickly discovered and exploited by wasps and may become exhausted before it has even been discovered by a honey bee, but a widely occurring nectar flow, even if limited in duration, will be in good time discovered by the searcher bee (Butler, 1951) and once this has happened great numbers of successfully alerted collectors will thoroughly exploit it in a manner which is far beyond the reach of the less populous wasp colonies.

Summary

In a comparison of foraging honey bees and wasps on syrup dishes certain conspicuous differences in individual behaviour reflected differences in the organisation of food exploitation by the two species. Wasps found dishes more quickly than bees, but unlike the latter they did not alert their colony mates and they were less constant to a particular dish. While searching wasps were less easily discouraged by rain or by deterioration of the food, they were more easily disturbed by the experimenter or by any moving object. The honey bee colony, with searching and collecting bees, is more efficient in the exploitation of rich uniform sources of food, while wasps are better equipped to deal with casual and more varied sources of food.

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The Influence of Exercise on the Selection of Food by Rats

By D. E. TRIBE

School of Veterinary Science, University of Bristol

Introduction

Whether or not animals are capable of selecting for themselves from the components of a balanced ration just those foods best suited to satisfy their nutritional requirements is uncertain. Although much of the relevant literature is confused and contradictory, it is nevertheless possible to draw one or two general conclusions from it. Firstly, it has been shown on several occasions that although an animal deficient in vitamins A, D or E may fail to select a diet containing those essential factors when given the opportunity to do so (Harris, Clay, Hargreaves and Ward, 1933; Wilder, 1937; Tribe, 1954) if deficient in the vitamin B-complex, rats show a remarkable partiality for diets rich in those vitamins (Harris *et al.* 1953; Richter, Holt & Barelare, 1938; Scott & Quint, 1946; Tribe & Gordon, 1953a).

Secondly, it is clear that there are a number of non-nutritional factors which may have a critical influence on an animal's food selection, and therefore feeding behaviour cannot be taken as an infallible guide to nutritional requirements (Tribe & Gordon, 1950, 1953b).

Thirdly, it is often assumed that whatever other relationship there may, or may not be, between appetite and physiological need, an animal will voluntarily adopt a calorific intake which is related to requirement and which therefore will vary with energy need and expenditure (Hausmann, 1932, 1933). The present experiment was designed to determine whether in fact the calorific intake of rats would vary with the amount of exercise taken by them.

Experiment

Four litters of hooded Lister rats which each contained three males and three females were divided into three equal groups of similar sex and littermate distribution. When the rats weighed approximately 150 g. they were placed in individual cages measuring $10 \times 10 \times 5$ inches. To the walls of each cage were wired three food containers which contained maize starch, glucose, and a basal diet composed of 46 per cent. casein, 34 per cent. margarine,

20 per cent. yeast, and a mineral and vitamin supplement. The calculated caloric values were maize starch, 3.5; glucose, 3.7, and the basal diet, 5.8 cal./g. The food containers were all identical in shape and colour, and in each was placed 15 g. daily of the appropriate food. The residues from the previous twenty-four hours were recorded daily and by subtraction the daily intakes of each food were calculated. A sheet of paper was placed beneath the wire mesh floor of each cage to collect any food scattered by a rat but this seldom amounted to an appreciable quantity. All rats received ample supplies of water and were weighed daily.

Each group was given three experimental treatments, A, B, and C, in the following way

Group No.

Group No.		
1	2	3
A	B	C
C	A	B
B	C	A

Each treatment was continued for fourteen days. Treatment A entailed no special exercise routine at all. During Treatment B each rat was placed in an exercise wheel for two thirty-minute periods each day, and during Treatment C each rat spent four such periods in the wheel each day. When one group of rats was being exercised those rats not due for such treatment were placed in a small empty cage in order to prevent them from eating during that time. Otherwise, when not being exercised the rats remained under the system of management already described.

The exercise wheel consisted of a wire-mesh cylinder which was mounted horizontally and in which there were twelve separate compartments. The dimensions of the cylinder were as follows: length, 72 in.; diameter, 21 in.; perimeter 66 in.; width of each compartment, $5\frac{1}{2}$ in. It was driven by an electric motor adjusted to give a speed of 12 r.p.m. which meant that during one thirty minute period a rat would travel approximately 660 yards. Thus, under treatment C the rats travelled approximately

TABLE I. The Average Daily Individual Consumption of Food in Calories for each Group for Each Week of the Experiment.

GROUP ONE						GROUP TWO						GROUP THREE					
Week Number	Treat-ment	Maize	Glucose	Basal	Total Calorie Intake	Treat-ment	Maize Starch	Glucose	Basal	Total Calorie Intake	Treat-ment	Maize Starch	Glucose	Basal	Total Calorie Intake		
1	A	21.3	12.4	24.8	68.5	B	21.3	10.0	39.4	70.7	C	21.3	5.2	41.2	67.7		
2		22.7	10.0	39.4	72.1		24.1	6.4	40.6	71.1		16.8	0.0	43.5	80.3		
Average		20.6	14.6	39.4	74.6		22.0	10.0	39.4	71.4		22.7	5.8	40.9	69.4		
3	C	15.7	10.8	36.5	63.0	A	22.7	7.2	44.1	74.0	B	25.9	7.2	42.9	76.0		
4		16.4	12.4	45.2	74.0		19.9	7.2	50.5	77.6		24.5	8.8	49.3	82.6		
Average		16.1	11.6	41.2	68.9		21.3	7.2	47.0	75.5		25.2	8.0	46.4	79.6		
5	B	18.9	15.2	46.4	80.5	C	22.0	6.8	42.3	71.1	A	29.0	9.2	49.3	87.5		
6		18.2	16.0	45.2	79.4		22.0	10.8	41.2	74.0		26.9	10.8	41.2	78.9		
Average		18.5	15.6	45.8	79.9		22.20	8.8	41.8	72.6		28.0	10.0	45.2	83.2		

1½ miles each day in addition to their normal activity in the food cages, under treatment B they travelled ¾ mile, and under treatment A they did not work at all. Of course, the latter statement is only theoretically true but it is certain that when placed in the very small cages without food they took very little exercise. During the exercise periods the animals were all observed and it is certain that the rats in the wheel did not cling to the side and revolve round and round, but did in fact stay at the bottom of the wheel and walk against its motion. After a few periods in the wheel they readily learnt to do this and it caused them no apparent stress or discomfort.

Results and Discussion

The average individual daily consumption of food in Calories, for each group, for each week of the experiment is shown in Table I. The figures make it plain that no statistically significant difference exists between the Calorie intakes of the same group during different treatments, or of different groups during the same period of time. In fact the uniformity of the results is their one outstanding feature. If the total average number of Calories consumed daily by the individuals of each group is added together for each fortnight of the experiment, irrespective of treatment, the following progressive increase is found, 215.4 Cals., 224.0 Cals., 235.7 Cals., which may be related

to the progressive increase in average body-weight throughout the experiment. If the total average number of Calories consumed daily by the individuals of each group is added together according to experimental treatment the following figure results. During treatment A 233.3 Calories were consumed, during treatments B and C, 230.9 and 210.9 Calories respectively were consumed. While this apparent trend of a decreased calorific intake related to an increased energy expenditure is not statistically significant it is quite obvious that the rats showed no inclination at all to correlate positively calorific intake with expenditure. The level of calorific intake from the outset was unexpectedly high; it would normally be anticipated that rats of this breed and weight would eat 15g. increasing to 20g. of stock diet (3.5 Cals./g.) per day, giving a daily intake of 52.5 Cals. rising with bodyweight to 70.0 Cals. Rats used by Richter *et al* (1938) on a self-selection system of feeding grew from an average of 120g. to about 190g. in bodyweight and during this period consumed an average of only 46.3 Calories.

Since the energy expenditure varied according to experimental treatment, and yet calorific intake remained constant throughout, it is to be expected that the rates of bodyweight increase would reflect the amount of exercise undergone. This is to some extent borne out by the results. Table II shows the average individual

Table II. The Average Individual Bodyweight Increase for Each Group for Each Week of the Experiment.

Week Number	GROUP ONE		GROUP TWO		GROUP THREE	
	Treatment	Bodyweight Increase g.	Treatment	Bodyweight Increase g.	Treatment	Bodyweight Increase g.
1	A	30.6	B	25.4	C	17.4
2		24.8		20.0		14.9
Total		55.4		45.4		32.3
3	C	10.8	A	30.7	B	30.6
4		16.0		24.5		27.1
Total		26.8		55.2		57.7
5	B	11.9	C	9.8	A	26.9
6		29.1		15.9		23.3
Total		41.0		25.7		50.2

bodyweight increase for each group for each week of the experiment. These figures make it clear that when receiving Treatment C the rats failed to consume sufficient Calories to maintain their normal rates of growth. To a lesser extent this is also true of Treatment B. The average individual bodyweight increase for the rats in all the groups was 53.6 g. during treatment A, 48.0 g. during Treatment B, and 28.3 g. during Treatment C. It is perhaps surprising that these differences were not larger but in this respect one or two other points must be borne in mind. Firstly, the difference in level of exercise between the treatments is not entirely reflected by the work done in the exercise wheel. When in the food cage for twenty-two hours out of every twenty-four, the rats under Treatment A were observed to move about a good deal while those under Treatment C were noticeably less active. Nevertheless, a substantial difference in energy expenditure must still have existed between the treatments. In the absence of precise information it is possible to conjecture that the heat output of the rats receiving no special exercise was higher than that of those undergoing Treatments B and C, and, therefore, part of their high calorie intake was dissipated in this manner instead of as work or growth.

Summary

Three groups each of eight hooded Lister rats were maintained on a self-selection system

of feeding and each group was submitted to three different levels of exercise. At no time did the voluntary calorific intake vary with the amount of exercise undergone. Instead the rate of bodyweight increase was slowed down as the amount of exercise increased.

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The Influence of Light and Touch on the Orientation and Behaviour of *Gonodactylus glabrous* Brooks

By NIELS BOLWIG

Department of Zoology, University of the Witwatersrand, Johannesburg

During a short visit to the Island of Inhaca, near Lourenço Marques, some experiments were carried out on the orientation of *Gonodactylus glabrous* Brooks. This Stomatopod usually hides under stones in the intertidal zone of the flats on the western side of the island, and it might be expected that light, as well as contact with objects in the water would aid orientation.

A. Reaction to Light

Experiment 1

Two pieces of slightly crumpled paper of equal size, one black and the other white, were placed in an aquarium illuminated from above. The reaction of each of 9 individual *Gonodactyli* were tested two or three times giving a total of 25 tests. In each test the animal was placed half way between the two pieces of paper with an axis at a right angle to the connecting line: in 24 cases out of 25 the *Gonodactylus* went to the black paper, and only once to the white.

Experiment 2

At low tide the *Gonodactyli* are found hiding under stones in water only 3-4 inches deep. If chased they immediately swim towards the nearest object and hide under it. In this experiment 10 animals hiding under stones were each twice given the choice between a lump of plaster of Paris and a lump of coal, both about two inches in diameter. Both were placed about eighteen inches from the animals' hiding places the one to the right, the other to the left. If in the first test the coal was placed to the left of the animal, it was placed on the right in the second test. In 20 tests with 10 animals, all went straight to the coal.

Experiment 3

If instead of using a piece of coal and a piece of plaster of Paris two pieces of coal were used, one 4 inches and the other 2 inches in diameter, 17 out of 20 went to the larger lump of coal.

It was noticed during Experiments 1 and 2 that the animals went towards the coal even if they had to swim towards the light to get there. This suggests the presence of skototaxis.

Experiment 4

A number of *Gonodactyli* placed in a tank with light from directly above swam with their dorsal sides up.

Experiment 5

With light from directly below the glass floor of the tank, the animals swam with their ventral sides up.

Experiment 6

With a horizontal beam of light the animals collected at the side furthest away from the light and showed a tendency to turn their backs towards the light. This behaviour is not necessarily a result of negative phototaxis or positive skototaxis. Dorsal light compass reaction combined with low thigmokinesis might lead to the same result.

Conclusion

The experiments give evidence of the presence of positive skototaxis and dorsal light compass reaction in *Gonodactylus*.

B. Contact with Objects

Experiment 7

If a number of *Gonodactyli* were kept in darkness in a tank containing objects under which the animals could obtain many contact points for their bodies, they collected under such objects. Those that failed to find the objects came to rest along the sides of the tank with their ventral sides inclined towards the perpendicular wall at an angle of 45° whereby they obtained symmetrical contact with their lateral sides. It was, however, found that the animals were more active in darkness than in light and showed a greater willingness to leave their hiding places. These observations were made in light flashes from a torch.

Experiment 8

It was noticed during the experiments with objects in nature that the animals swam straight towards the lower edge of the selected one, and then when touching it with their antennae took up a position parallel with its surface. Their ventral sides were inclined towards the

object. If an object that offered only few contact points was presented to an animal it swam along it touching it with its legs until it came to a projecting angle, when it would leave the object, turning towards the side—away from the surface it had followed (See Fig. 1).

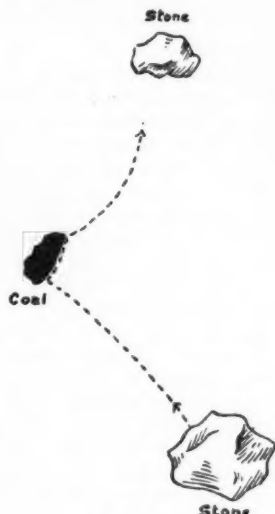


Fig. 1

Experiment 9

If the animals were placed in a hollow in the sand filled with water, they swam about for a short while being unable to find enough contact points. Eventually they turned on their sides, rolling themselves up with their abdomens tucked in under the thorax.

Conclusion

Gonodactylus shows low thigmokinesis. It is necessary for the ventral as well as both the lateral sides of the animal to be in contact with the object. Observations seem to indicate that it is the contact between the legs and the object, rather than that of the body that is of importance.

C. Reaction to Light and Contact Combined

Experiment 10

A number of *Gonodactyli* placed in a tank illuminated from above were found to swim over the bottom touching it with their legs. At

the side of the tank they inclined themselves with their ventral sides towards the side wall. They did not place themselves at an angle of 45° to the perpendicular, as they would have done in darkness; but at an angle somewhat smaller. It seemed likely that the position taken up was caused by a compromise between the reaction to the light from above, and the thigmokinetic response to the bottom and the perpendicular wall of the tank. Of the three posterior thoracic appendages, the one in the middle was bent under the body while the two others were stretched out to the side.

Summary

The experiments on the reactions of *Gonodactylus glabrous* to light and to touching objects show that:

1. It swims towards dark objects even if thereby it has to swim towards the light (skototaxis).
2. Darker objects are preferred to lighter objects.
3. Bigger objects are preferred to smaller objects.
4. In perpendicular light it exhibits a dorsal light compass reaction.
5. It comes to rest when it has many ventral and lateral contact points (low thigmokinesis).
6. It is more active and willing to leave its hiding place in darkness than in light.
7. There is a characteristic compromise in the reaction when light and touch are combined as stimuli acting on the animal in different directions.
8. Light and touch are two stimuli which trap the *Gonodactylus* under stones and under other objects during the day. When the intensity of light falls to a minimum during the night the animals become less bound to their hiding places and are able to leave their shelter and swim about.

Acknowledgment

I am indebted to the Portuguese Maritime Commander, Capt. Moreira Rato, for the facilities given, and for granting me permission to stay at the Marine Biological Station on Inhaca, off Lourenço Marques.

Responses of *Locusta migratoria migratorioides* (R. & F.) to light in the laboratory

By R. F. CHAPMAN

Birkbeck College, London

The need for accurate information on the responses to light of *Locusta migratoria* was repeatedly realised in the course of a study of its behaviour in relation to micro-climate. An investigation was therefore made in the laboratory of the photokinetic and phototactic responses of the nymphal (hopper) stages.

Photokinesis

All field observations on this aspect of locust behaviour are open to the criticism that changes in light intensity are usually accompanied by temperature changes, which themselves affect behaviour most markedly. The only laboratory work specifically intended to show the different levels of activity of locusts in light and darkness is that of Edney (1937). Using an actograph in a constant temperature room at 27°C., he found that *Locusta* adults showed much more activity in light than in dark. His adults were reared from hoppers subject to alternating periods of 12 hours' light and 12 hours' darkness, but he did not work on the hopper stages or at lower temperatures. This is of some importance since locusts in the field can rarely be subjected to a night temperature of 27°C., and the change from darkness to light, which is of interest from the point of view of first movements of hoppers in the field, commonly takes place at temperatures much lower than 27°C. Bodenheimer (1929), using *Schistocerca gregaria* (Forsk.) in an actograph, gives a figure (his Fig. 25) which shows a quiescent period at night with activity in the day, but he related the quiescence entirely to low temperature without considering the change in light intensity. Key (1936) and Grassé (1922) have casual laboratory observations, and Kennedy (1939) and Pielou (1948) describe some field observations and experiments which suggest that differences in light intensity correspond with differences in locust activity (positive photokinesis).

Apparatus

An actograph was constructed along the usual lines, balanced on knife edges and actuating a lever which recorded on a smoked drum. The

cage was eight inches long and one and a half inches square in cross section; the width allowed a fifth-instar hopper to turn freely without permitting much lateral movement, which would not be recorded. The cage was made entirely of sheet cellulose acetate, so that light could enter equally in all directions. This material is smooth and prevented the animal from climbing the walls. The floor of the cage was freely perforated; this enabled the hopper to obtain a firm foothold and also facilitated the free passage of air through the apparatus, so reducing to a minimum humidity changes caused by the animal. The cage alone was enclosed in a large box lined with white paper but open above to the white ceiling of the room. The only other opening in the box was the slit through which the lever worked. In this way the possible stimuli presented to the insect were reduced to a minimum. Light was supplied by the ordinary ceiling light which was six feet away from the apparatus, and on a level with the top of the enclosing box. The only light entering the box was therefore that reflected from the ceiling so that the intensity of illumination was comparable on all sides but rather greater from above, and phototactic responses were virtually impossible. For dark periods, the whole room was kept in complete darkness. The room was maintained thermostatically at 20°C., and the arrangement used ensured that the electric light could not possibly affect the temperature of the hopper in the apparatus.

Experiments

Since it is well known that the internal physiological state of hoppers is important in behaviour studies, and since the aim of the experiments was to investigate the possibility of photokinesis acting in the field in the mornings, an attempt was made to reproduce the internal state of the hoppers at that time. A cage of fifth-instar hoppers was therefore kept without food from the morning until the late afternoon, when food was provided so that by 18.00 hours the hoppers had had every oppor-

tunity of being well fed, as they would be in the field in the evening. A single hopper was then taken at random and put into the cage of the actograph. The light was immediately turned out; it was turned on twelve hours later by a time switch. It was hoped that, when the light came on in the morning, the internal state of the hopper, with regard to hunger, temperature and light adaptation, would resemble the state of hoppers in the field at dawn. The experimental conditions differed from field conditions in that the change from darkness to light was a sudden one.

The results (Fig. 1) showed that in all of 15 cases tested, more activity occurred in the light than in the dark, no activity at all taking place in the dark in eight of these. Since the temperature was constant at 20°C. throughout the experiments, the change in activity might be due to hunger, positive photokinesis, or an inherent rhythm of activity.

Four hoppers were tested in light at 22°C. in a manner similar to that described above. These records showed (Fig. 2) that the period of quiescence after feeding, Ellis's (1951) post-prandial period, was of the order of three hours, being $2\frac{1}{2}$, $2\frac{1}{2}$, $2\frac{1}{2}$ and 3 hours for the four hoppers. A fairly high state of activity was reached after about $3\frac{1}{2}$ hours. This left no doubt that the change in activity observed in the previous experiments when the light was turned on was not correlated with the end of the post-prandial period of quiescence. Excessive starvation resulted in a high level of almost continuous activity, but such a state was not reached for some 36 hours after the last feed.

In a further series of experiments, the light and dark periods were reversed so that 12 hours' light was followed by 12 hours' darkness. In five out of five cases, the activity occurred mainly in the first 12 hours although the degree of hunger was increasing (Fig. 3). The effect of this complete reversal of light and dark periods further indicated that no inherent rhythm of activity was involved.

These experiments leave no doubt that hoppers of *Locusta* are more active in light than in darkness at 20°C. under otherwise constant conditions, provided the degree of starvation is not too great.

Phototaxis

It is fairly well established that Acrididae exhibit a positive movement towards light. However, no experiments have been described for *Locusta*, and the majority of those for other

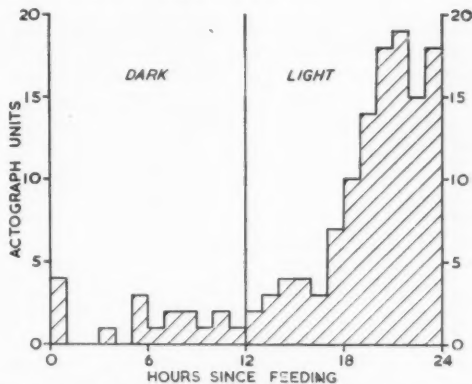


Fig. 1. Total activity of 15 fifth-instar hoppers in the actograph over a 24-hour period, showing greatest activity in the light.

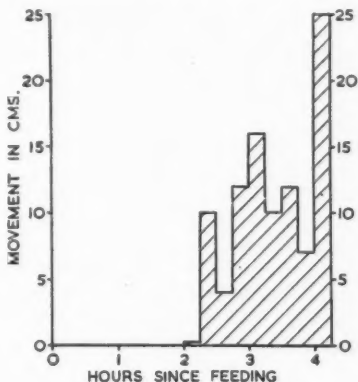


Fig. 2. Activity of four fifth-instar hoppers in the actograph after feeding, showing the post-prandial period of quiescence.

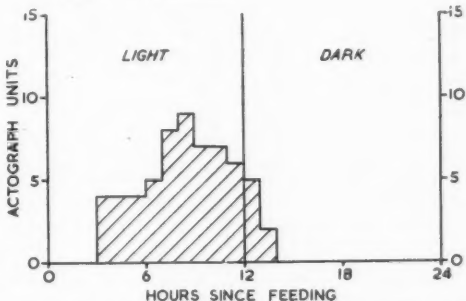


Fig. 3. Total activity of five fifth-instar hoppers in the actograph over a 24-hour period, showing greatest activity in the light.

Acridids are open to criticism in some respects. Laboratory experiments have been carried out by Fraenkel (1929) on *Schistocerca*, Rubtsov (1935d) on several species of grasshoppers, and Grassé (1922, 1923) on *Anacridium aegyptium*, *Aeolopus strepens* and *Chorthippus (Stauroderus) bicolor*. The only apparatus fully described is by Grassé, and in all his experiments the insects were started at the end furthest from the light so that any movement was inevitably towards it. In the present experiments, hoppers were dropped into the centre of the apparatus.

Apparatus

A cage (Fig. 4) 18 inches long by four inches wide and six inches high was made with a gauze floor, and with sides and top of cellulose acetate so that hoppers could not climb up. For control experiments in darkness and to minimise interference by the observer, a system of indicator lights (door lights) was arranged so that when the hopper reached one end of the cage a small light at that end flashed on. To achieve this, the cage was fitted at each end with a very light door, also of cellulose acetate, which was hinged above. Each door was balanced so that the pressure of a fourth- or fifth-instar hopper against it would cause it to swing out. This completed an electric circuit and the door light flashed on at whichever end of the cage had been reached by the hopper (Fig. 5). The whole of the cage was surrounded by a black screen so that the observer was

completely hidden, and reflected light reduced to a minimum. A lamp box was placed at each end, opposite the ends of the cage but outside

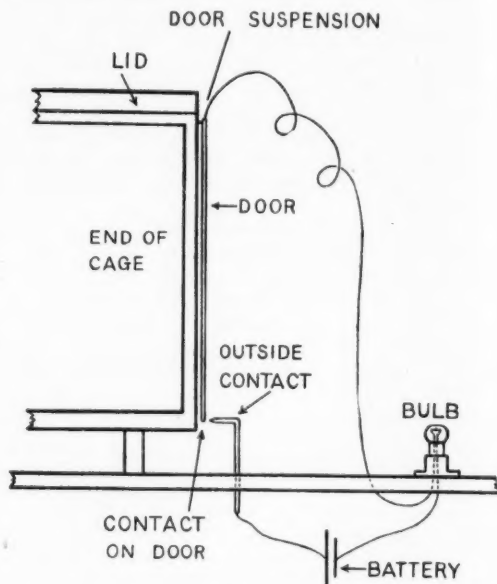


Fig. 5. One end of the test cage shown in Fig 4 to show the 'make-and-break' in the circuit by which the arrival of a hopper was indicated.

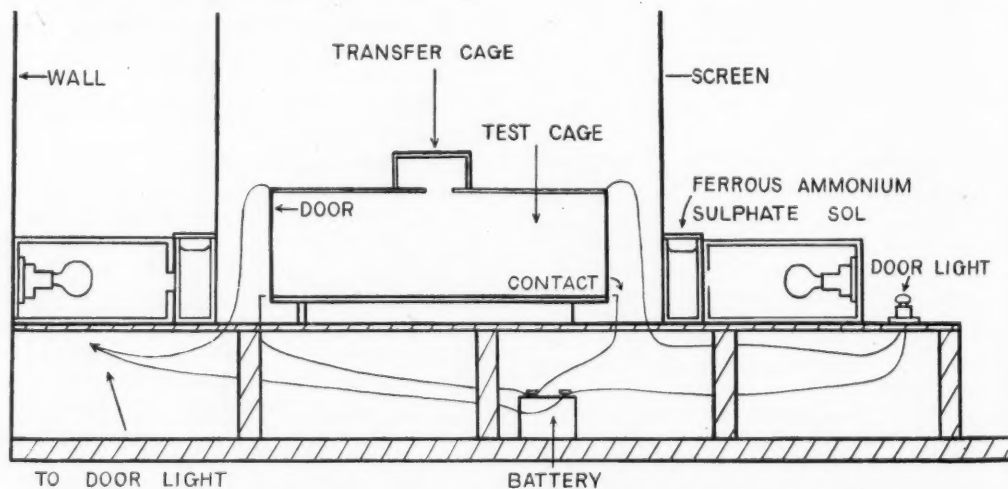


Fig. 4. Diagram of the apparatus for testing the photo-tactic response of hoppers.

the screen, which was cut away here. Radiant heat was reduced as far as possible by using only a 60-watt bulb and by placing a trough containing a solution of ferrous ammonium sulphate (Pantin, 1946) between the lamp box and the screen (Fig. 4). A check on the efficiency of the radiation screening showed that no temperature changes were induced in the apparatus by the use of the light. By the random use of the lights at either end, any possibility of the hoppers learning to turn in a certain direction was eliminated.

Experiments

For the experiments, fifth-instar hoppers were in a dark-adapted state at temperatures varying between 25 and 28°C. Each hopper was subjected to ten trials with one light, the other light and no light used in a random sequence. The tests in complete darkness were used as controls to ascertain whether hoppers preferred one end of the cage for some unknown reason. Hoppers, which were tested singly, were introduced into the apparatus from a small box with a sliding floor, on withdrawal of which they fell through a hole in the roof into the test cage. The switching on of one of the lights was synchronised with this fall. Each test lasted a maximum of five minutes, the hopper being removed if it had not reached one end of the cage in this time.

Altogether 265 tests were carried out in complete darkness as controls. Of these, in 91 cases the hopper went to one end, in 104 to the other, and in 70 it remained motionless in the middle section of the cage until five minutes had elapsed. This showed that movement in darkness was random ($p > 0.05$). In a similar number of tests in unidirectional light, the hopper went towards the light in 196, away from it in 18, and remained motionless in 61. There was no doubt that the hoppers showed a positive movement towards the light ($p < 0.01$).

Like other reactions, the reaction to light depends on the general physiological state of the hoppers. Fraenkel (1929) and Grasse (1922) found that phototaxis became feeble above 30°C. and Hussein (1937) obtained no response to light in *Locusta* below 15°C., at which temperature cold stupor began. Facilities were not available for extending the present work to include the effect of temperature on photo-taxis.

Some experiments were carried out on the effect of age within the instar on phototactic responses. Some fifth-instar hoppers were

marked and tested ten times each day throughout the instar. The graph (Fig. 6) shows that the response reached a fairly high level after three

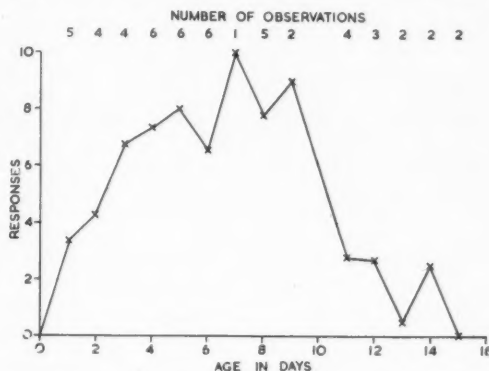


Fig. 6. Variation of the phototactic response with age. The number of responses is an average of the positive movements towards light made in ten tests each day and based on the number of observations shown along the top.

days and remained high until the ninth day, after which it fell off, this being correlated with the proximity of the final moult.

It was this effect of age which was the cause of some of the null results obtained in the experiments on phototaxis. It was found that hoppers which stayed in the centre of the cage once usually did so several times. Some of these were isolated, and they moulted to become adults within two days of the tests. In others it is possible that the inactivity resulted from recent feeding. Newly moulted hoppers were never used, so that low activity following the moult did not affect the results.

In a final series of experiments, a red filter (Evans Electroselenium No. 204 transmitting 7200Å to 6400Å, diminishing to zero at 5600Å) was interposed between the lamp box and the screen. Seven fifth-instar hoppers were tested ten times each, and the direction of the light reversed after every five tests. Of these 70 tests, 29 gave no result after five minutes, 34 gave positive results, and 7 gave negative ones. Ignoring the tests that gave no results, the three hoppers concerned being particularly inactive, the results were significant ($p < 0.01$) and indicated that hoppers of *Locusta* are sensitive to light of the wave-length used.

All the experiments so far described were on fifth-instar hoppers, which were tested individ-

ually. Mass tests of the other instars were made in a simple cage of zinc gauze 18 inches long with cellulose-acetate top and ends. This was placed inside the screen instead of the other cage. The floor was marked off into six sectors, each three inches long. Large numbers of hoppers were introduced at a time and then given five minutes complete darkness to settle down. At the end of this time, a diffuse light above was turned on and the number of hoppers in each sector was counted. The count was repeated after ten minutes of unidirectional light. By subtracting the first count from the second the displacement of hoppers was found. Each instar was tested at least ten times, and no group of hoppers was used more than once. A clear positive movement towards the light occurred in all cases (Fig. 7).

A few experiments were carried out to see how well the phototactic behaviour corresponded with one of the named categories of behaviour (Fraenkel & Gunn, 1940). Unilaterally

blinded hoppers performed circus movements towards the seeing side, on a white sheet of paper in a darkroom, with a 40-watt bulb three feet above the paper as the source of illumination. Lowering the bulb increased the intensity of illumination and there was then an increase in the rate of turning in the two hoppers tested in this way (Table I). No means of measuring light intensity was available. Circus movements of this kind indicate a tropotactic element in the behaviour.

At each of two adjacent corners of an 18-inch square of white paper, ruled in inch squares, was a 2.5-volt light bulb. Hoppers were started

Table I. Rate of Turning of Unilaterally-blinded Hoppers in Different Light Intensities.

Intensity in arbitrary units	1	1.8	4	7.1	16	28.5
Angle turned per inch	16.5	22.8	36.0	46.9	49.1	35.6

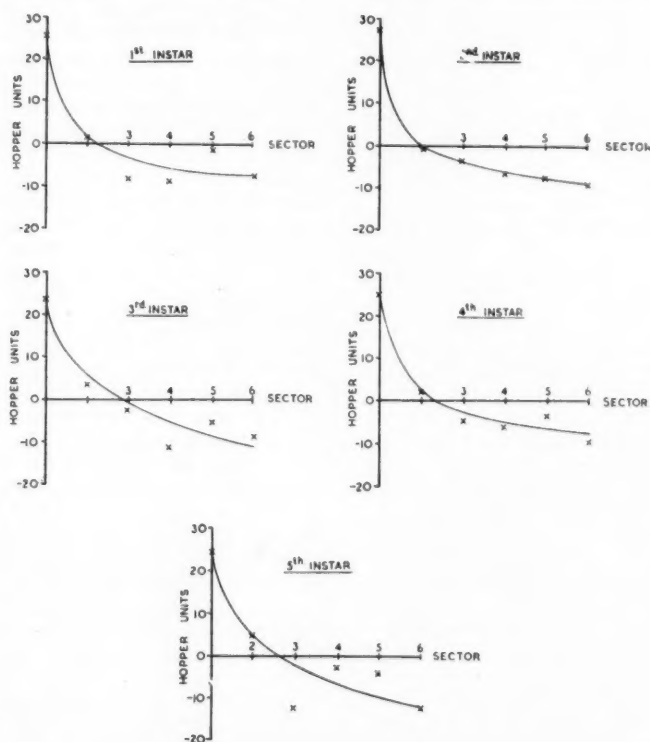


Fig. 7. Results of the mass phototaxis experiments, showing a positive movement in all instars.

from the side of the square opposite the lights. The experiments were carried out at temperatures below 20°C . so that the hoppers were not too active. The paths of the hoppers were plotted on graph paper. With two equal lights very few hoppers walked more than 10° outside the angle subtended at the starting point by the lights, and they were very evenly distributed over this sector towards and between the two lights (Fig. 8). Cancelling left by right, the mean angle of divergence from the median path was 2° . In unequal lights, the hoppers showed a strong tendency to go towards the stronger light (Fig. 9), the mean path angle being displaced 12° towards the brighter light. The angles were measured four inches from the starting point, so that they show the direction in which the insect started; they are not confused by the curve to one light or the other shown in most tropotactic behaviour (Fraenkel & Gunn, 1940). Observation of the individual paths showed some (7 in 65) with abrupt discontinuities in the line of movement, hoppers changing from orientation towards one light to orientation towards the other. This type of behaviour is characteristic of telotaxis (Fraenkel & Gunn, 1940).

Unilaterally-blinded hoppers were tested in the two-light experiment and all moved towards a light. Out of 12 cases, five exhibited circus movements, making at most three turns before moving towards a light, and then walked without further circling. One hopper, having reached one light, walked straight across to the other. This ability to move straight towards a light when unilaterally blinded suggested that the hoppers are not dependent on a tropotactic mechanism alone, but have a telotactic mechanism available.

Summary

1. It was shown by means of an actograph that, at constant temperature, hoppers of

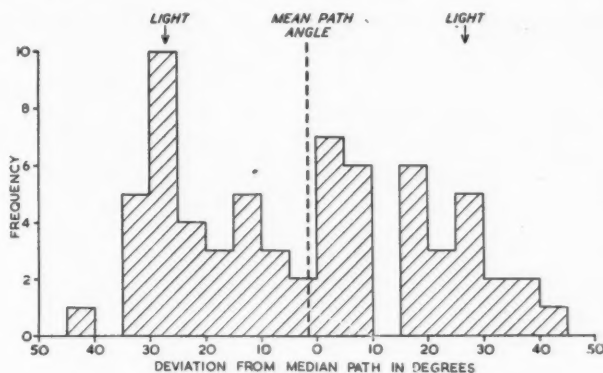


Fig. 8. Paths of fifth-instar hoppers in the two-light experiment with lights of equal intensity.

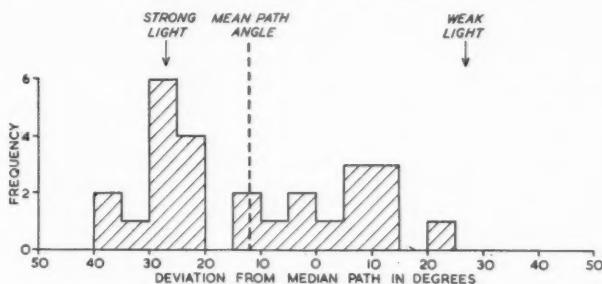


Fig. 9. Paths of hoppers in the two-light experiment with lights of unequal intensity.

Locusta migratoria migratorioides are more active in light than in darkness.

2. The period of quiescence after feeding was about three hours in light and much longer in darkness. Activity began with light, and not as an independent diurnal rhythm.

3. An apparatus in which the phototactic response was investigated is described.

4. Hoppers of all instars showed a positive movement towards the light. The intensity of this response was greatest in the middle of the instar. Hoppers appeared to be sensitive to red light.

5. Unilaterally blinded hoppers performed circus movements in a uniform light, the rate of turning increasing with light intensity.

6. In experiments with two lights, some hoppers went straight to the lights, others between them. Unilaterally blinded hoppers moved straight towards a light, sometimes

after some initial circus movements. It is concluded that both tropotactic and telotactic mechanisms are available.

Acknowledgments

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An Automatic Recording Maze for Insect Behaviour Studies

BY P. T. HASKELL

Department of Zoology and Applied Entomology, Imperial College Field Station

During research on the effect of the sensory receptors of insects of the Order Orthoptera on their spontaneous locomotor activity, an apparatus was required which would record such activity over long periods. Actographs of the type described by Gunn & Kennedy (1936), Cloudsley-Thompson (1953), and Hammond (1954) suffer from the disadvantage that the space available for movement is necessarily somewhat restricted. Furthermore, in the particular experiments envisaged it was desirable to be able to use a maze to allow learning experiments to be carried out.

Therefore mechanical methods of recording activity, either directly, as in the actographs referred to above, or indirectly, as with the apparatus of Eayrs (1954) and Pavan (1952), are ruled out. Amongst alternative methods the "sound actograph" of Park (1937) suffers from the great disadvantage of requiring a sound-proof cabinet, and the final choice must be between mechanisms operated photo-electrically or by capacitance relay. These can be arranged to close a relay on passage of an insect across a light beam or capacity plate; the closures may be counted, giving an index of activity. Although the mechanisms can be arranged to operate when an insect passes in a given direction, this is a needless complication when it is only desired to record total activity. Siddorn (1950) has used the photo-electric method to monitor the activity of ants in an artificial nest, and Backlund & Ekerood (1950) describe an apparatus based on the capacitance method for use as a field actograph. The circuitry of both these methods is fairly complicated and it was finally decided to develop a simple photo-electric circuit. The method finally chosen also lends itself to registration on a simple printing recorder, which can give continuous recording over a period of weeks. Ancillary apparatus which produces and controls any desired changes in environment can be made to record on the printer, thus giving complete data for any experiment on one sheet of paper.

General Plan of Apparatus

Figure 1 shows the various electrical units of the apparatus. Each unit except the electronic chart recorder is built into a standard 19-inch rack mounting panel and the whole is assembled in one standard 5ft. rack. This arrangement allows ease of manipulation and maintenance. The activity in the maze is monitored by the cold cathode counter unit (Unit D) which feeds the information to the printer (Unit F) via the printer relay unit (Unit E). The temperature and illumination of the maze can be pre-set by the cycling unit, (Unit C) and information about these changes is also fed to the printer for recording. Measurement of temperature and humidity in the maze can be made at any time by Unit B, and measurement of illumination at the surface of the maze is made by a photo cell with a calibrated micro-ammeter located in Unit C. Any one of these variables may be recorded continuously over 24 hours on the electronic chart recorder (Unit A). The printer relay unit will print the derived information at $\frac{1}{4}$, $\frac{1}{2}$ or 1-hour intervals according to its setting. For longer or shorter reading intervals than this some form of external timing is required. The printer will record up to one month's results at a reading interval of one hour without the need to change paper or printing ribbon.

The panel at G, Fig. 1, is the main fuse and distribution panel for A.C. mains.

The Maze

Figure 2 gives an idea of the lay out of the maze, which is constructed of sheet copper bent to form a channel of $1\frac{1}{2}$ -inch square cross-section, and is closed at the top by sections of thin window glass. It is desirable to have the glass in several sections to enable parts of the maze to be uncovered separately. The whole maze is fixed to a sheet of 14 gauge aluminium, which is mounted on a shallow metal or wooden box containing heaters (Fig. 2 A). The high thermal conductivity of the aluminium mounting sheet and the maze material itself gives rapid

equalisation of temperature all over the maze even when heating is somewhat unevenly distributed.

The maze and its heating box are mounted on sponge rubber pads to reduce vibration and the whole installed in a large cabinet (Fig. 2). This is constructed of hardboard on a wooden frame. One side of the cabinet is hinged to allow access to the maze and adjustable ventilating louvres are provided in two opposite walls. The cabinet has a false ceiling made of removable wooden battens in which sheets of ground glass or other light diffusing material may be placed (Fig. 2 D). Above this diffuser is a removable box top in which are mounted several lamps (Fig. 2 E).

Photocell and Lamp Assembly (Fig. 2 B)

Infra-red light was used to activate the photocell since this is not visible to most insects and will not therefore attract or repel them. This is simply obtained by capping the projection lamp and lens system with an infra-red filter; this lamp unit is mounted on an adjustable stand so that it can be extended over any part of the maze. On the same stand is mounted the photo cell (Fig. 2 B). This is a G.E.C. CMG 22 A cell mounted in a light-tight box with a lens system.

The beam from the lamp is projected on to a mirror assembly placed on the floor of the maze, from which it is reflected on to the photo cell. The mirror is held in position by two bent copper strips which restrict the pathway in the maze at this point to about 1 inch wide. In this way, insects with marked thigmotaxis which would otherwise keep to the sides of the maze are forced to pass over the mirror.

Cold Cathode Counter (Fig. 1 D)

The counter to be described is based on the Ferranti cold cathode triode K.32. The chief difficulty encountered in this apparatus was the relatively slow interruption of the beam. Under such conditions cold cathode thyatrons may fire and not recover, thus putting the counter out of action. This may be overcome first by arranging the H.T. supply to the valve to be kept at optimum value by a large condenser, which when discharged by one interruption of the beam takes several milliseconds to recharge, and second by having an oscillatory circuit in the valve anode. Although this arrangement cuts down the maximum possible counting speed, this is still of the order of 2 counts per

second, which is far higher than the maximum needed in practice.

The basic circuit of one counter is shown in Fig. 4 D; in the actual unit (Fig. 1 D) two counters are built into the same chassis, a common meter monitoring the L.T. and H.T. supplies.

When the light beam falling on the photocell is interrupted by passage of an insect over the mirror, the voltage on the grid of the valve increases and it fires. The valve is kept from blocking by the oscillatory circuit in its anode, consisting of the L.F. choke and condenser in series. The initial current pulse caused by interruption of the light beam operates relay B/1. Although not shown in the circuit diagram, one pair of contacts on this relay operate a G.P.O. message counter at every closure, and thus the unit may be used as a simple counter or monitor as it stands, without further apparatus.

A delay network associated with each G.P.O. counter enables a delay time of up to 6 seconds to be introduced during which the counter is inoperative. This is a useful feature for eliminating "spurious counts" caused by two appendages of the same insect interrupting the light beam separately.

An H.T. supply rheostat and meter enables the supply to be set at a figure which allows the counter to work satisfactorily over the range of mains voltage fluctuations which occur at the place of use.

Cycling Unit (Fig. 1 C)

This unit contains the apparatus for the heating and lighting of the maze and for the cyclical control of these factors. The basic circuit diagram of the unit is shown in Fig. 4 C. Control of heating is by a thermostat mounted on the maze and a hotwire vacuum switch in the unit. Power supply to the vacuum switch is controlled by a relay B/2. This is in turn controlled by the auto/manual switch S 2. When at manual the heat is on constantly, the final maze temperature being controlled by the thermostat setting. When S 1 is set at auto, the main supply to the heaters is controlled by the cycling device, which will be described below.

Control of lighting is similarly by relay A/2 and auto/manual switch S 2; rheostat R 1 enables intensity of illumination to be changed. Light intensity at the surface of the maze is monitored by a photocell (Fig. 2 C) reading on a

PLATE I

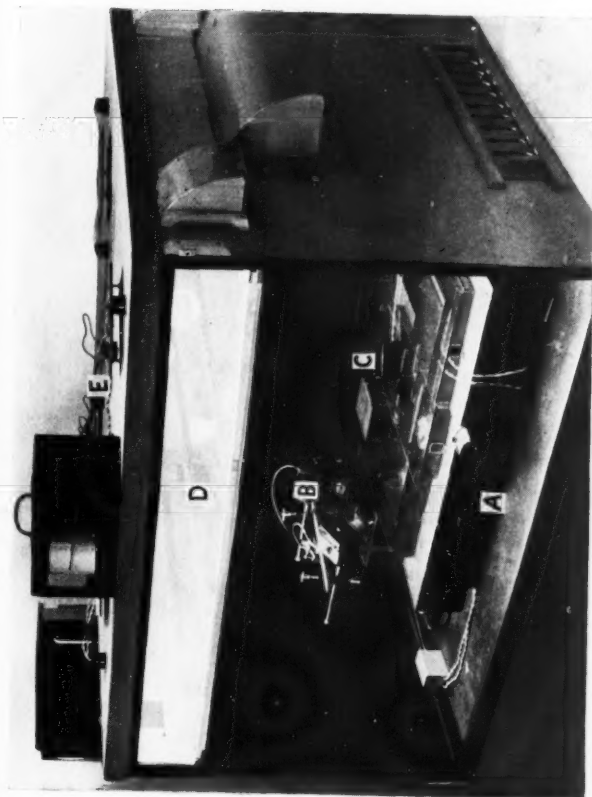


Fig. 2. Maze and Cabinet: for description see text

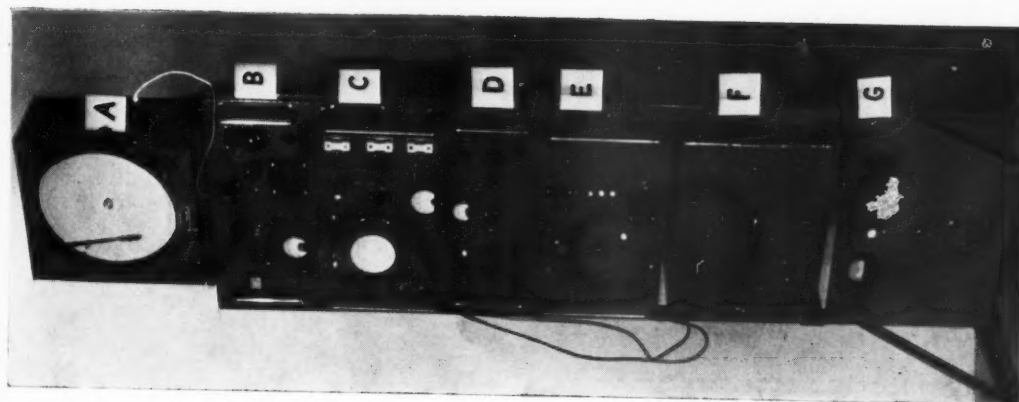


Fig. 1. Electrical units and racks: for explanation see text.

PLATE II

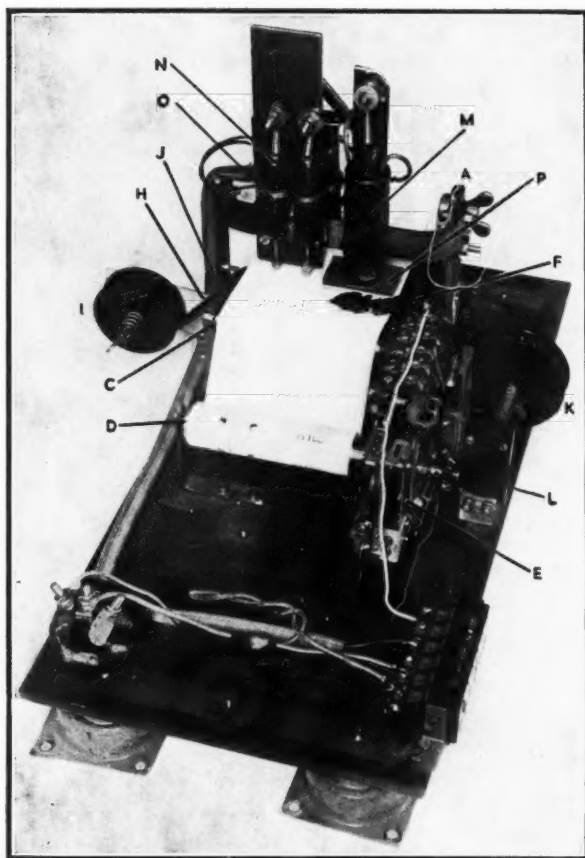


Fig. 3. Printer Unit, removed from case: for description see text.

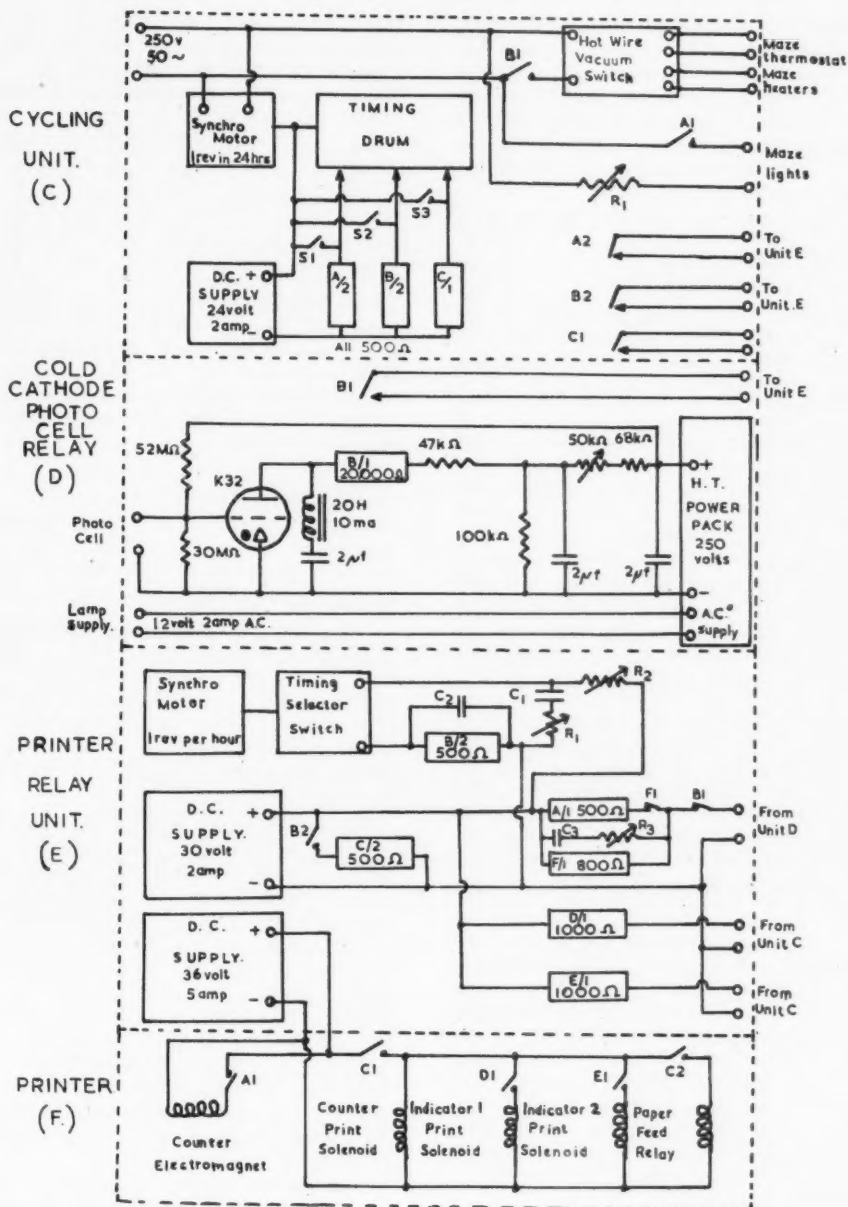


Fig. 4. Simplified circuit diagram of apparatus. All relays shown in the non-operated condition. For explanation see text.

microammeter mounted on the cycling unit. This is calibrated in foot candles and enables illumination of the maze to be set accurately. The output from the maze photo cell, which is a barrier layer type, may be taken directly to the electronic chart recorder, and thus a continuous 24-hour record of light fluctuations in the maze can be obtained.

Heat control relay B/2 and light control relay A/2 have secondary contacts brought out to jack sockets; if these contacts are connected to the inputs of the Indicator units on the Printer Relay Unit these indicators will operate all the time the relays are made, and thus will produce a mark on the data sheet indicating the beginning, duration and end of periods of heating and lighting.

The cycling device itself consists of a 4-inch diameter brass drum driven by a self-starting synchronous electric motor at a speed of one revolution every 24 hours; the drum is earthed through the motor spindle. Trailing on the surface of the drum are three light wire contacts, held against it by gravity assisted by light springs. Contact with the drum completes the relay circuits via earth and the relays operate; if, however, the contacts are prevented from touching the drum by placing a strip of paper over it, the relays will only operate when holes in the paper enable the contacts to touch the drum. Thus a paper strip will control the "programme" of the relays over a period of 24 hours, according to the position and length of the holes cut in it. Advantages of this method of control are that programmes for several periods may be prepared beforehand, can be changed in one minute, and can be kept for record purposes and future use.

Relay C/1 is a relay, its contact being wired to a jack socket on the front panel, which gives a control facility depending on the programme. It can be used for operating special stimuli in the maze, such as sound or vibration, or for releasing by electromagnetic switch quantities of food or water in feeding experiments. It can also be used to give timed release of insects into the maze for learning experiments. By utilizing one of the Indicators operated from the Printer Relay Unit, such activities can be recorded on the printed data sheet.

Temperature and Humidity Measurement Unit (Fig. 1 B)

Temperature measurement is carried out with thermistors in a balanced bridge circuit. The

thermistors used are Standard Telephone: type KB 2322/80 is used to measure the temperature of the flat metal surface, and type F 2311/300 is used for air temperature measurement inside the maze.

These are selected by a switch and feed into a normal Wheatstone bridge circuit, with a centre zero galvanometer and variable potentiometer, the slow motion dial of which may be calibrated directly in degrees Centigrade. Accuracy is to within $\pm \frac{1}{2}^{\circ}\text{C}$.

Humidity measurement is by the capacity resistance hygrometer of Jason (1953). The sensitive element, which may be made as small as a matchstick, can be introduced inside the maze without interfering with conditions. The meter is calibrated directly, reading percentage relative humidity.

The outputs of either the temperature or humidity bridges may be connected to the electronic chart recorder, which will then give a continuous 24-hour record of temperature or humidity variations in the maze.

The Printer Unit (Fig. 3)

The units described above feed information to the Printer Relay Unit, which in turn feeds it to the Printer. The Relay Unit also provides the power supply for the printer. Fig. 4 E & F, gives the simplified circuit diagrams of both these units while Fig. 3 is a photograph of the printer, from which its simple construction may be appreciated.

The rolls of paper used are housed on an axle assembly, with a spring tension device to keep the paper taut. (Fig. 3 A). The paper is led over paper guide C and is collected on the take-up roller D. This roller is driven directly by the impulse relay E, which is so wired that every time it operates the roller D turns through a $\frac{1}{4}$ -revolution. The paper guides channel the paper over the printing counter, F. In Fig. 3 the paper is cut away to show the counter. This is a 5 digit non-resetting printing counter type E.S. 2834 made specially by W. Lethaby & Co. The counter is operated by an adjustable link mechanism from an electromagnet mounted beneath it.

The printing medium is heavily inked type-writer ribbon (H) drawn from a supply reel (I) over the ribbon guide (J) between the counter and the paper; the take up spool for the ribbon (K) is driven by a bevel reduction gear (L) from the impulse relay (E) and is moved on

about one $\frac{1}{4}$ -inch for every reading made. Since one winding of ribbon lasts for a month at one reading per hour, no automatic re-winding arrangements have been made, and the ribbon is re-wound by hand when the supply spool is nearly empty.

Printing is done by the printer Solenoids M, N, & O. Solenoid M is the counter printer, and, when energised, forces the rubber faced printing platen (P) down onto the paper against the ribbon and the numbers on the counter. A very clear print is obtained, an example of which can be seen on the paper in Fig. 3. Solenoids N & O are the extra "indicator" printers, and merely make marks with their small circular printing platens, by forcing the paper and the ribbon against the ribbon guide J.

The whole chassis is mounted on anti-vibration supports and encased in a metal-housing running on extending arms attached to the rack; this makes removal for maintenance or repair very simple.

Printer Relay Unit (Fig. 4 E)

Fig. 4 E gives the simplified circuit diagram of the printer relay unit. The 30 and 36-volt power supplies are conventional transformer and bridge rectifier circuits.

The timing apparatus centres round a 250 v., 50-cycle synchronous motor which has a speed of one revolution per hour; during one revolution it closes a contact at each quarter hour. The "Timing Selector Switch" enables any of these contacts to be paralleled; with them all in parallel, switching occurs at every quarter of an hour; with two opposite contacts in parallel, switching occurs at half hourly intervals; with one contact only in circuit, switching is hourly. One of the problems with mechanically operated time switching is that the "make" period of the contact is long compared with the time needed to complete the operations of printing and paper feed. These latter take about three seconds, while the smallest reliable "make" period on the contactor is of the order of half to one minute. During the period of printing and paper feed, the photo counter must be put out of operation, or it might operate the counter while this is printing; the period of one minute is too long for the counter to be out of action, so the problem arises as to how to get a short "make" period (about one second) from a pair of contacts which close and remain closed for a half to one minute. The following relay arrangement is used to perform this task (Fig. 4 E).

A condenser C 1 (250 microfarads) and a variable resistance R 1, (20,000 ohms) in series are fed from the 30-volt supply, through a limiter resistance R 2 of 20,000 ohms. Across the condenser resistance network are placed the relay B/2 and the timing selector switch contacts. When the D.C. supply is switched on, the condenser C 1 will gradually charge up through the resistors R 1 and R 2. When the contacts of the timing switch are made the condenser will discharge through the relay B/2, causing it to operate. When the condenser discharge is complete, the relay will reset, because although the timing contacts are still on the "make" period, insufficient current to operate the relay can pass the limiter resistance R 2. While the timing contacts are still made, the relay acts as a shunt to the condenser, which cannot charge up, so there is no chance of spurious operation. When, finally, the timing contacts open, the condenser begins to charge again and is available to operate the relay at the next reading period. The actual length of time for which relay B/2 operates can be adjusted by varying capacity C 2; with the values "given" relay B/2 closes for about one second.

The cycle of events occurring on closure of relay B/2 can be followed on Fig 4 E. Firstly, contact B 1 opens and renders inoperative the counting circuit. Then contact B 2 closes; this causes operation of relay C/2. Contact C 1 closes first and causes the counter printer solenoid to operate, printing the reading. If the indicator trip relays D/1 and E/1 have been operated by inputs from the cycling unit, then closure of contact C 1 will also cause printing of marks by these indicators. Contact C 2 closes after C 1 and causes the paper feed relay to operate, moving the paper along ready for the next printing. The whole operation of printing and feeding the paper forward takes about two seconds.

The remaining circuit to be considered is the counter circuit. Closure of the relay in the cold cathode relay unit completes the circuit of relay A/1 through the 30-volt supply. On closure of contact A 1, the counter magnet operates the counter. However, a slow moving insect or an insect stopping on the photocell mirror, might cause a succession of impulses to reach relay A/1 and consequently a number of spurious counts will be made. A circuit is required which allows the first impulse of a series of impulses to pass, but stops the remainder; this

is afforded by relay F/1, the counter guard relay. Relay F/1 is slugged so as to be slow-to-operate, and is placed in parallel with relay A. With a single impulse coming from the relay unit, F/1 does not operate; if more than one impulse occurs, then F/1 has time to operate and in so doing opens contact F 1 and makes relay A/1 inoperative, thus isolating the counter circuit. The resistance capacity network C 3 (1000 microfarads) and R 3 (5000 ohms) which shunts relay F/1, allows a variable delay of up to six seconds to be put on the restoring of contact F 1.

Electronic Chart Recorder (Fig. 1 A)

The recorder used is a Fielden Servograph Type RL1. This instrument records on a chart rotating at one revolution in every 24 hours the movements of a 50-microamp D.C. meter. Outputs from the humidity and temperature recorders and from the photocell monitoring illumination on the maze, can be connected to this recorder to obtain records of these factors over a period of 24 hours.

Capabilities of the Apparatus

The aim has been to make the apparatus as flexible as possible to enable it to be used in a number of problems and with different animals. The size of the maze is of course a limiting factor, but the principle may be applied to animals of very different sizes. Many different types of information can be obtained from the apparatus, such as measures of spontaneous activity, activity resulting from application of various stimuli repeated at any desired rate or intensity, measure of choice between two given stimuli, measure of learning ability either by individuals or by number of animals. By arrangements of the two photo cell counters, speed of movements or frequency of movements of given lengths can be recorded. Furthermore, as has been mentioned before, experiments may be continued for as long as a month, with readings taken every hour, without the need to replace paper or printing ribbon, and all the important data for one experiment are contained on one roll of paper. One slight disadvantage of the counter is that it is not of the re-setting type, that is, it does not return to zero between readings. Thus for quantitative experiments, the number

of counts in a given period is obtained by subtracting the two figures printed at the beginning and end of the period. At the time this apparatus was built (1952) no suitable counter was available, but at present (1954) the True-meter Company of Manchester have on the market an electric printing re-setting counter which would be ideal for this type of work.

Apart from behaviour experiments calling for the use of the maze, the electrical units and maze cabinet provide a "controlled environment" which may be used for other types of behaviour experiment or for breeding.

Acknowledgments

I should like to record my thanks to my colleague, Mr. J. W. Siddorn, for helpful discussions on various technical points and for taking photographs of the apparatus, and to Dr. J. T. Eayrs, Department of Anatomy, University of Birmingham, for kindly reading the manuscript.

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Book Reviews

Ways of the Ant. By JOHN CROMPTON. London: Collins. 1954. Pp. 254. 15s.

Mr. Crompton sets out to clear up some of the popular misconceptions about ants—and termites. He embarks on a description of ant life which adds nothing to the accounts of past authors. His extreme anthropomorphist way of writing seems to kill the very wonder that he hopes to rouse for he falls into the error of using his false human analogy so much that one almost forgets that the book is about ants. He is lead into superlatives that are quite unwarranted by the facts. The wonder lies not in the complexity of the human behaviour to which ant behaviour is so often paralleled but in the simplicity of the basic patterns which by combination and interplay can yield the many sided social organisation which he seeks to describe. Perhaps this book will lead some people to keep their eyes wider open than usual and check for themselves the observations described. But above all, to quote the author's preface, "The reader must not be too literal minded—that is all!"

J.D.C.

Bird Migrants. By ERIC SIMMS. London: Cleaver-Hume Press, 1952. Pp. 212. 15s.

In his introduction the author says that "the book is naturally built on the foundations supplied by many authorities and is intended to draw together a number of the threads of recent study and relate them to the final patterns of migration." To one who has no special knowledge of the subject, but is deeply interested in it, "Bird Migrants" provides both interesting and informative reading and the reviewer believes that the author has, in large measure, succeeded in accomplishing what he set out to do. The scope of the work is indicated by the ten chapter headings: The Form of Migration, Birds on the Wing, Birds as Navigators, Seen and Unseen Migration, Movements on Broad Fronts and Narrow Routes, The Cross Roads of the Air, Inland Migration, The Cotswold Corridor, The Cotswolds in the Spring, Fact and Fiction. The text is embellished by fine photographs, maps and diagrams. There is a comprehensive bibliography and index.

C.H.-S.

A Thousand Geese. By PETER SCOTT and JAMES FISHER. London: Collins. 1954. Pp. 240. 25s.

This is an enthrallingly interesting and informative book which reflects in its every page the unquenchable enthusiasm of the members of the Severn Wild Fowl Trust expedition to Iceland in 1951. The object of the expedition was to trace the main breeding grounds of the Pinkfoot. The majority of the world's Pinkfeet are to be found in England and Scotland during the winter months but considerable doubt existed as to where they nested—was it in Greenland, Iceland or Spitzbergen? Observations made in Spitzbergen suggested that only a small fraction of the world's population nested there. In Greenland there is a wide distribution of geese on stretches of tundra that become free of snow but there are far too few birds in both those countries to account for the known winter population of some thirty to forty thousand. It was believed that more than half of the gross population might nest in Iceland. To test this belief the present Expedition set out from Reykjavik on the 22nd June, 1951. As the expedition proceeded to the interior plateau observations were made on other species, and these, the difficulties encountered, the disappointments and the excitements, are all faithfully recorded in a most entertaining way. But the main theme is directed to the search for breeding Pinkfeet and the reader will begin to see how fruitful the expedition's activities were in this connection as he reaches the closing chapters. The authors conclude that the Icelandic breeding ground is probably the greatest in the world. Five valuable appendices follow the main account. These deal with the pinkfoot in Spitzbergen and in Greenland, there are notes on the birds of the *Iðjarsárver* vid Hofsjökul (reprinted from the fifth Annual Report of the Severan Wildfowl Trust, a plant list of the Pteridophyta and Spermatophyta compiled by Finnur Gudmundsson (also reprinted from the same Annual Report) and finally a further reprint from the Trust's Report on the probable pinkfoot population of the *Iðjarsárver* vid Hofsjökul in 1951. The book concludes with a bibliography of works on the distribution and habits of the pinkfoot. One always expects much from these authors and one is never disappointed.

C.H.-S.

The Herring Gull's World. By N. TINBERGEN. London: Collins. 1953. Pp. 255, 51 photographs, 58 drawings and diagrams. 18s.

Dr. Tinbergen's recipe for the study of a new species is first observation, and then observation, experiment and comparison. In this masterly analysis of the life of the Herring Gull he allows us to see his technique in action: no one interested in animal behaviour can afford not to read it.

The greater part of the book is devoted to the reproductive behaviour of the Herring Gull and demonstrates clearly the importance of observation in the analysis of behaviour. Of course it is not sufficient for the observation to consist merely of the collection of facts—reading this book one can see how Dr. Tinbergen's success depends on constantly asking the right questions ("Even an hour's careful observations of the goings on in a gullery faces one with . . . more problems . . . than one could hope to solve in a lifetime."), and on continually analysing the facts which he collects to answer them.

These questions are not confined to the immediate causation of behaviour—though this is the central theme—but are also concerned with its significance in the life of the bird and its elaboration during the course of evolution. These three approaches combine to give an all-round and extraordinarily vivid picture of the Herring Gull's world. In particular, the analyses of threat and courtship behaviour, which have already set the pattern for similar analyses in other species, are of special importance: these alone would suffice to make this a book of reference for a long time to come.

Later in the book Dr. Tinbergen describes some experimental work designed to elucidate how Herring Gull's "recognise" their eggs, and to analyse the stimuli which release the pecking of the chick. These experiments are a development of the observational analysis—they were made in the field and, unlike so many experiments on animal behaviour, are related to the normal life of the bird.

Throughout, Dr. Tinbergen frequently compares his findings with those obtained from other species. This comparative approach both facilitates the analysis of the behaviour in question, and enables the generality of the conclusions to be assessed.

As well as being of outstanding importance for students of bird behaviour, this book is a

pleasure to read. It is written with great vividness and charm: the gulls are real gulls, not biological abstractions, and the problems are meaningful ones.

The 51 photographs are technically excellent; further, they are not just a collection of the "parent bird at nest" type, but a carefully organised record of the behaviour patterns discussed. As a collection they must be unique.

R.A.H.

An Analysis of the Parental Behaviour of the Male Three-spined Stickleback (Gasterosteus aculeatus). J. J. A. VAN IERSEL. Behaviour. Supplement No. 3. Pp. 1-139.

For many years a handful of species—Dogfish, Cockroach, Frog, Rat, Sea Urchin, *Drosophila* and a few others—have, in their several fields, been the classic animals of Zoology. Now, as a result of the work started by Dr. Tinbergen and carried on by his pupils and colleagues at Leiden University, the Three-spined Stickleback has joined them. Only a small section of this work has so far been published, and Dr. van Iersel's monograph is the first detailed study to appear.

Once the male stickleback has settled on a territory, three fairly distinct phases in the reproductive behaviour can be recognised—nest-building, sexual, and parental. Each is marked by the frequent occurrence of certain characteristic activities. In this work the factors causing the change from the sexual to the parental phase are elucidated. The method used is, in principle, simple: the amount of "fanning" (the behaviour by which the male aerates the eggs in the nest) is used as an index of parental activity; and the number of zig-zag dances (a courtship activity) given in a standard time to a standard stimulus as a measure of the sex drive. Various external factors are manipulated (in particular the number of times the male is allowed to fertilize, and the number and age of the clutches in his nest) and their effects assessed.

Dr. van Iersel applies this method with extraordinary effectiveness. The relentlessness with which he analyses the problem and then tracks down and elucidates one relevant factor after another should serve as an example for all future experimental work of this type. The argument, though necessarily complicated by the thoroughness of the analysis, is clearly set out: at every stage the evidence for each deduction is presented and due notice taken of alternative interpretations.

Only a very brief summary of the principal conclusions reached in this admirable study can be given here. The fanning drive is released and primed by the eggs, the effect depending on the age of the eggs. The act of fertilisation depresses the sex drive and facilitates the building up of the fanning drive. The sexual and parental drives exert inhibitory influences on each other.

This paper is an important milestone in experimental ethology by virtue both of the important contribution which it makes to the understanding of instinctive behaviour, and of the high standards which Dr. van Iersel has set—which future workers would do well to try to emulate.

R.A.H.

The Heron. By FRANK A. LOWE. London: Collins. 1954. Pp. xiii + 177, 1 colour plate, 15 photographs, 13 drawings and maps. 18s.

This "New Naturalist Special" volume provides an important survey of the life cycle of

Ardea cinerea. It is based largely on the author's own experience, gained through many hours of field study, supplemented by a careful analysis of the literature on the species. The result is a very valuable collection of facts which should provide a useful background for more detailed studies of this interesting bird—though many readers would find the facts more palatable if they had been placed in biological perspective by some more detailed hints as to their theoretical significance.

R.A.H.

Im Reiche der Fischreiher. By KURT GENTZ. Dresden: Sachsenverlag. 1952. Pp. 112. 67 plates. 7.50 D.M.

A collection of photographs of marsh birds, most of which are of moderate quality. Some interesting observations are embedded in the text, which is largely of the "meine gefiederten Freunde" variety.

R.A.H.

BOOKS RECEIVED

The following books have been received, and in appropriate cases will be reviewed as space permits in early issues:

Reginald Appleyard.

Geese: Breeding, Rearing, General Management 3rd Ed. London: Poultry World, Ltd. 3s. 6d.

W. H. Dowdeswell, (1952)

Animal Ecology London: Methuen & Co., Ltd. 12s. 6d.

James Fisher & R. M. Lockley (1954)

Sea-Birds London: Collins (New Naturalist Library) 25s.

A. Starker Leopold & F. Fraser Darling (1953)

Wildlife in Alaska New York: Ronald Press Co. \$2.75

R. M. Lockley (1953)

Puffins London: J. M. Dent & Sons, Ltd. 18s.

Helen Mellanby (1953)

Animal Life in Fresh Water: A Guide to British Fresh Water Invertebrates

London: Methuen & Co., Ltd. 12s. 6d.

John W. Moyer (1953)

Practical Taxidermy: A Working Guide New York: The Ronald Press Co. \$3.00

Clifford B. Moore (1953)

Ways of Mammals in Fact and Fancy New York: The Ronald Press Co. \$3.50

Henri Piéron (1952). Translated by M. H. Pirenne & B. C. Abbott.

The Sensations: Their Functions, Processes and Mechanisms

London: Frederick Muller, Ltd. 42s.

N. Tinbergen (1953)

Social Behaviour in Animals London: Methuen & Co., Ltd.

New York: John Wiley & Sons, Inc. 12s. 6d.

David Wechsler (1952)

Range of Human Capacities Baltimore: Williams & Wilkins Co.

London: Baillière, Tindall & Cox, Ltd. 31s. 6d.

Karl Von Frisch (1954)

The Dancing Bees London: Methuen & Co., Ltd. 16s.

V. A. Rice, F. N. Andrews & E. J. Warwick (1953)

Breeding Better Livestock London: McGraw-Hill Publishing Co., Ltd.

34s.

- The Duke of Bedford.
Homing Budgerigars
1st. Ed. London: Cage Birds. 2s. 6d.
- A. I. Oparin (1953). Translated by S. Morgulis
Origin of Life
New York: Dover Publications, Inc.
Cloth: \$3.50. Paper: \$1.70.
- L. F. Whitney (1953)
All About Guppies
Connecticut: Practical Science Publishing Co.
\$1.50
- Bob Elliot (1954)
All About Brook Trout from Maine to California
Connecticut: Practical Science Publishing Co.
\$2.95
- I. W. Rhys.
Chick Management: From the Day-old Stage
5th Ed. London: Poultry World, Ltd. 1s.
- Denys Weston.
The Budgerigar in Captivity
13th Ed. London: Cage Birds & Bird Fancy.
3s. 6d.
- C. G. May.
Natural Hatching and Rearing
3rd Ed. London: Poultry World, Ltd. 1s.
- C. A. House & A. W. Smith.
Norwich Canaries
1st Ed. London: Cage Birds 3s. 6d.
- Keith Wilson
A Handbook to Poultry Practice
London: Poultry World. 10s. 6d.
- Wm. Marshall, 1st Ed.
Egg Incubation
London: Poultry World. 2s. 6d.
- Advisory Staff of "Poultry World", 1st Ed.
Egg Production in Laying Cages
London: Poultry World. 4s. 6d.
- Reginald Appleyard, 4th Ed.
Ducks: Breeding, Rearing, Management
London: Poultry World, Ltd. 5s.
- Leon F. Whitney & A. B. Underwood (1952)
The Raccoon
Connecticut: Practical Science Publishing Co.
\$3.75
- Earl Schneider (1954)
All About Parrakeets
Connecticut: Practical Science Publishing Co.
Inc. \$1.50
- Gerald M. Durrell (1953)
The Overloaded Ark
London: Faber & Faber, Ltd. 15s

ANIMAL BREEDING ABSTRACTS

This journal covers the world's published research on breeds, breeding, productivity, growth, genetics and reproduction of all farm livestock, poultry, fur bearers and other animals of economic importance, as well as the small laboratory animals. It also publishes a review article in each number. Volume 23 No. 1 will be published on 26th March.

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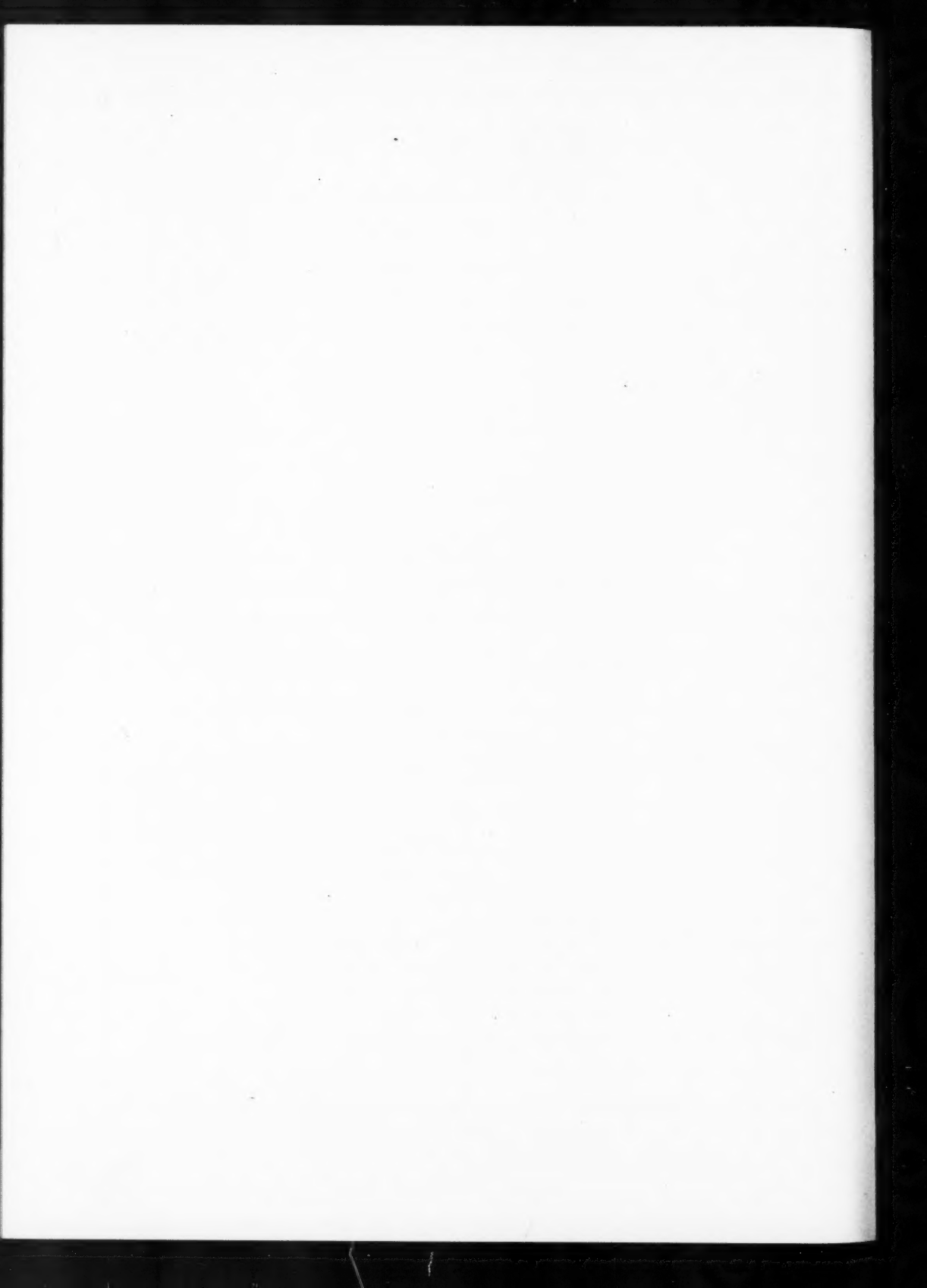
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The Association for the Study of Animal Behaviour is a scientific society, founded in 1936. Its aim is to promote and co-ordinate work in animal behaviour, the study of which is of interest or importance to a wide range of biologists, e.g., those engaged in psychology, physiology, zoology, animal husbandry and veterinary science.

Scientific meetings are held, often in conjunction with other societies, and the Association possesses a library from which members may borrow, and to which all members are asked to contribute copies of their publications. From 1936 to 1952 the Association published at irregular intervals the BULLETIN OF ANIMAL BEHAVIOUR. This has now been replaced by a regular quarterly publication, the BRITISH JOURNAL OF ANIMAL BEHAVIOUR, which contains original scientific papers and reviews.

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